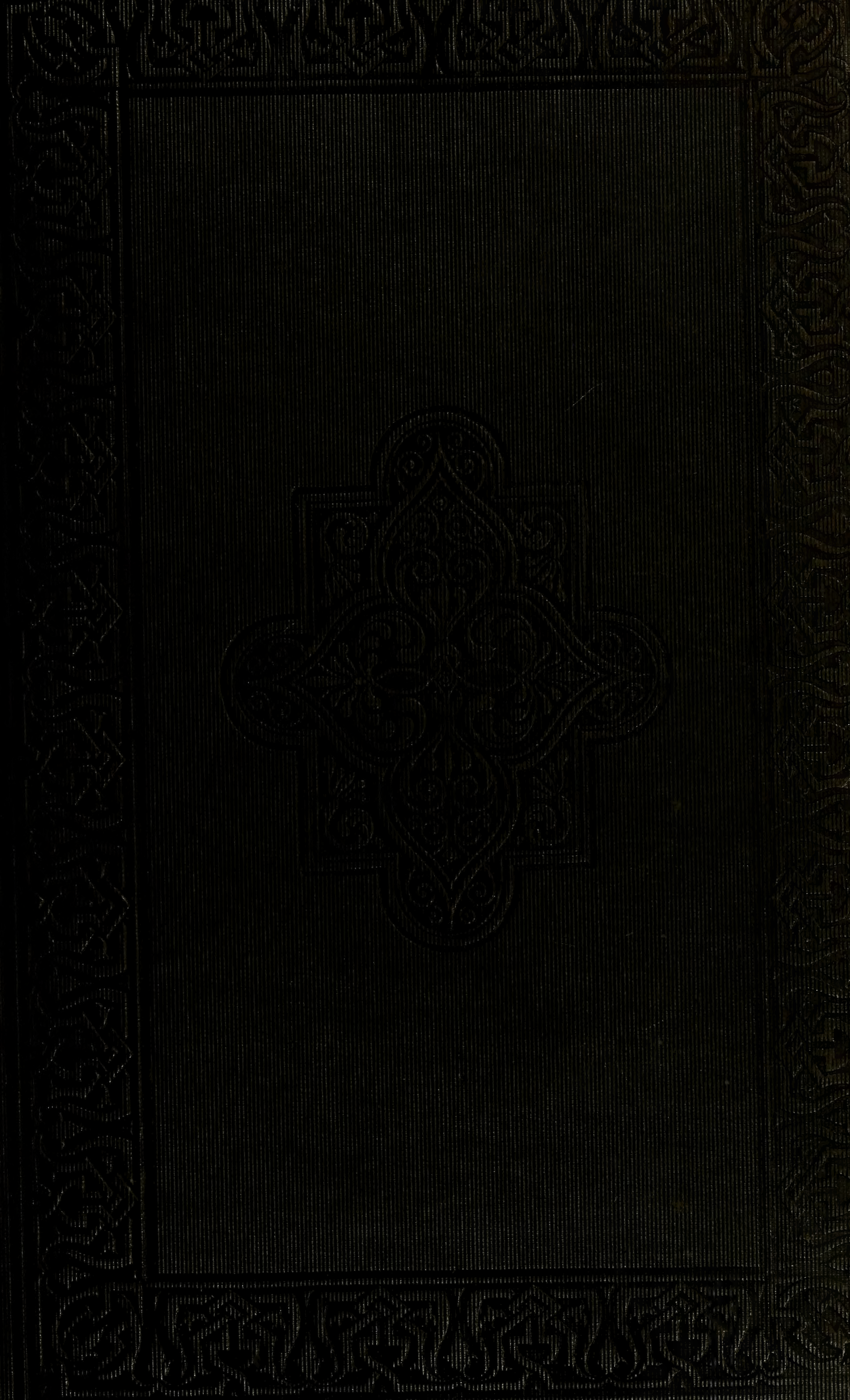

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EMBRYOLOGY,

WITH THE

PHYSIOLOGY OF GENERATION.

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EMBRYOLOGY,

WITH THE

PHYSIOLOGY OF GENERATION.

BY J. MÜLLER, M.D.

PROFESSOR OF ANATOMY AND PHYSIOLOGY IN THE UNIVERSITY OF BERLIN, ETC.

TRANSLATED FROM THE GERMAN,

WITH NOTES,

BY WILLIAM BALY, M.D., F.R.S.

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AND LECTURER ON FORENSIC MEDICINE AT ST. BARTHOLOMEW'S HOSPITAL.

ILLUSTRATED WITH STEEL PLATES, AND NUMEROUS
WOOD ENGRAVINGS.

(*From Müller's Elements of Physiology and Supplement.*)

LONDON:
TAYLOR, WALTON, AND MABERLY,
UPPER GOWER STREET, AND IVY LANE, PATERNOSTER ROW.
1848.

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The present Volume, taken from MULLER'S ELEMENTS OF PHYSIOLOGY, is issued separately, in consequence of its having been suggested to the Publishers that the subjects contained in it would interest many who might not wish to purchase the entire work. To render it complete, the corresponding portion of the Supplement, published in March 1848, has been added.

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EXPLANATION OF PLATE III.

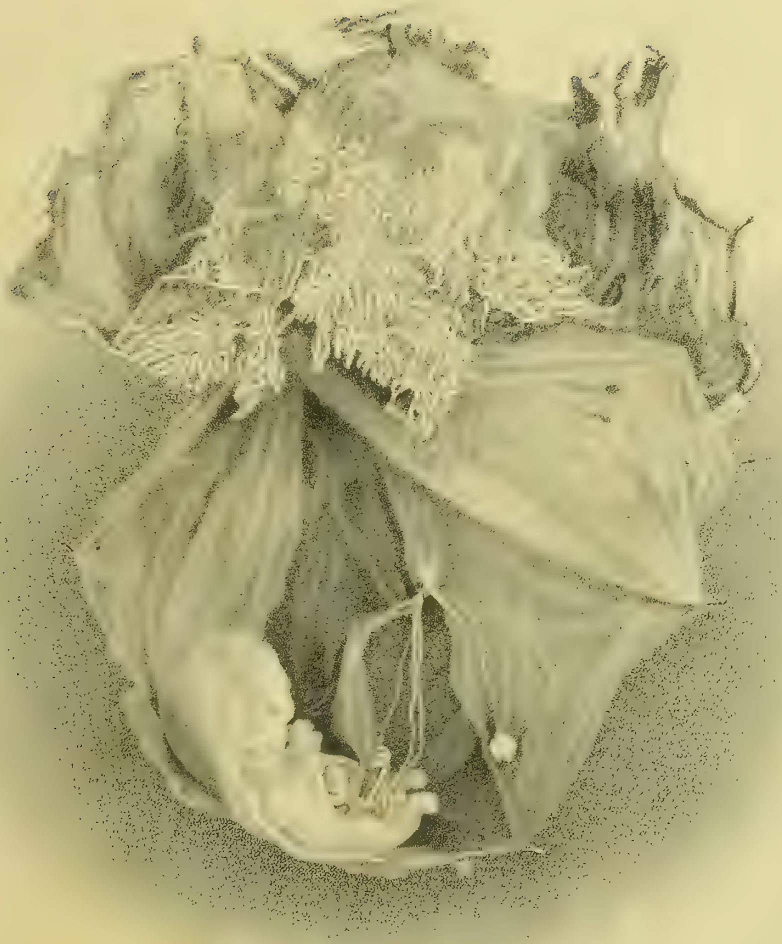
[This is the drawing of an embryo with its membranes, in the possession of Dr. Sharpey, of which an outline copy and a full description are given in the note at page 1581.]

EXPLANATION OF PLATE IV.

[Figures 1, 2, and 3, are drawings of the ovum and embryo to which reference is made by the author at page 1587.

Fig. 4 represents the second embryo belonging to Dr. Sharpey, described in the note at page 1582.

Fig. 5 represents the mesentery and intestine of the embryo shown in plate iii., spread out so as to display the mesenteric vessels and the origin of the omphalo-mesenteric artery from one of the main branches. See the description in the note at page 1581.]



DRAWN BY J. HASLOCH _ ENGRAVED BY CHARLES WASS.

PUBLISHED BY TAYLOR & WALTON, UPPER GOWER STREET,

LONDON, 1848.

Fig. 2.

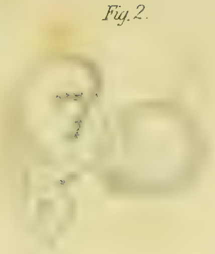
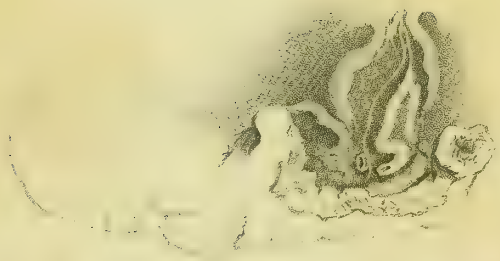


Fig. 3.

Fig. 4.



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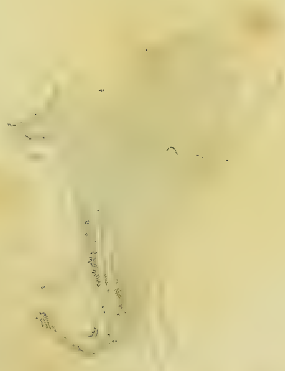


Fig. 1.

Charles Wass, sc.

London: Taylor & Walton, Upper Gower Street, 1848.

BOOK THE SEVENTH.

Of Generation.

SECTION I.

Of homogeneous or non-sexual generation.

CHAPTER I.

OF THE MULTIPLICATION OF ORGANIC BEINGS IN THE PROCESS OF GROWTH.

a. In Plants.

On a superficial comparison of the fully developed state of plants with their earliest condition, it is manifest that during their growth the organs which compose them undergo a multiplication, and that parts, which in the very young plant exist singly or in small number, are in the full-grown plant exceedingly numerous. The stem has sent out branches; and these branches have again given off side branches, to which they bear the same relation of central axes that the original stem bears to them. The leaves, also, which were at first very few, have undergone a manifold increase. A more attentive examination, however, soon shows that in this process something more than a mere multiplication of the organs of a single individual has taken place; and that, in fact, the full-grown plant consists of a system of individuals,* of a multiple of the vegetable organism which constitutes the plant in its earliest condition. This is demonstrated by the properties which parts of this compound system separated from the rest display. A branch of such a plant, separated from the stem and set in the ground, presents all the characters of the parent organism, and continues to live, nourishing itself and increasing. Even a subordinate portion, or twig, cut from this branch, manifests exactly the same properties. A portion cut from the end of the axis of very many plants, provided it contain stalk and leaves, will vegetate, and serve to continue the species. Now, the part separated from the parent stock in these instances, and still continuing to grow, most closely resembles the young plant in the condition in which it appears when first developed from the seed; and since each of the similar parts which together constitute a tree may be regarded as a young plant, endowed with the power of vegetating so as to form a large tree, so the fully developed tree itself must be viewed as a system of individual vegetable organisms associated together, and exerting a reciprocal influence on each other during their life, but yet separable as independent beings. The stem of a plant is the common fasciculus in which all the separate individuals are bound together. Hence it is that the thickness of the stem diminishes from below upwards in proportion to the number of branches given off; and by minute anatomical investigation it is revealed, that not merely the pith or medulla of the stem is continuous with that of the branches through the medium of the medullary rays, but also that the vessels entering into the composition of all the young twigs are prolonged downwards through the stem towards the roots. Every new development of leaf-buds throughout the tree is attended with the formation of a new stratum of vessels, corresponding to these leaf-buds, in the stem, while the older layers undergo the process of lignification. But although the prolongation of the vessels of each young sprout, through the stem to the root, is essential for the nutrition of the individual sprouts, and for their common life, yet it is not a necessary element in their individuality; for, when a twig is cut from a tree, it is separated from the greater part of its downward prolongations, and nevertheless constitutes a young plant, capable of developing itself to a compound vegetable system like that of which it formed part. The vessels of which we are speaking, as being prolonged from the individual twigs or sprouts to the roots, have their origin in the leaves; and the leaves, therefore, must be the parts in which the property of individuality more peculiarly resides. It is true most leaves will not develop themselves to perfect plants; but the principle is sufficiently established by the fact, that the leaves of many plants placed in the ground may be made to vegetate. This is the case, for example, with the leaves of the lemon, orange, Ficus elastica, and other plants; leaf-buds are developed at the margin of these leaves in the same way as they are ordinarily formed on the stems of plants. The leaf, therefore, must be regarded as an individual organism, containing in "essence" or "potentially" all that is comprehended in our notion of the species of plant to which it belongs, and capable of propagation by the development of branches. Almost all the organs of plants, indeed, are leaves; even the different parts of the flower are shown by the theory of the metamorphosis of parts to be leaves modified in form and function. On the other hand, however, the stem itself, when stripped of all its leaves and branches, cannot be looked upon as an aggregate of mere imperfect fragments of individuals. In this truncated condition the stem is still a multiple of the germ. For leaf-buds may be developed and sprout even from a stem thus truncated. All these facts, therefore, confirm the truth of the proposition, that the fully developed plant is a multiple of individual plants,—a compound system of individual organisms, the essential parts of which are certainly contained in the leaves, though they exist also in the stem when stripped of its leaves.

---

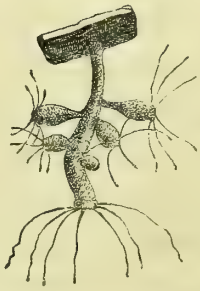
* Darwin, Phytonomia.

b. Animals.

The power of multiplying the vital force resident in the germ is not peculiar to plants. Animals, and it would seem all animals without exception, possess the same property. There are many instances in the animal kingdom in which the multiplication of individuals in the process of growth is quite as distinct as in vegetables; but in other cases it can be proved to take place, only by induction from a series of facts. The young polype developed from the ovum or gemmule of a compound polypiferous animal is at first a single individual, actuated by a single independent will. But in proportion as this young creature appropriates to itself new matter and grows, it becomes transformed into a multiple system of individuals, like that presented by a full-grown plant, and is then evidently regulated in its movements by many distinct centres of volition. A common stem unites all the component simple animals, and in the Sertularia the cavity of this stem communicates with the cavity of each polype, while out of its wall new polypes sprout. Those compound polypes which consist of a mere aggregate of independent simple animals united into one mass, are not referred to in the foregoing description.

One of the simple fresh-water polypes, or Hydræ, also, may, as we have learned from Trembley's observations, be transformed in the process of growth into a system of individuals analogous to a plant, with the exception that in the case of the compound Hydra the elementary parts of the young polypes are not continued in an isolated manner through the trunk of the parent individual, and that the digestive sacs of all form part of one common cavity. Each of the individual polypes composing the compound Hydra [Fig. 144] is actuated by an independent will; may be separated from the rest; and is, in form at least, a perfectly simple animal.

Fig. 144.*



Thus far we have considered only those organisms which in their compound state, attained by growth, consist of a system of individuals not merely "potentially," but "actually;" the separate members of the compound system having each its proper structure and independent will.

We now proceed a step further, and find animals which in form appear perfectly simple, and have only one directing will, but nevertheless are systems of parts endued with individual life, and capable of propagating

---

* [Figure of a polype multiplying in the process of growth, after Trembley, Mémoires pour l'histoire des polypes pl. viii. fig. 7.]

the form and organisation of the species. In these animals the component parts or segments undergo multiplication during the process of growth, and a certain number of them becoming separated, whether spontaneously or artificially, preserve the faculty of individual life. The parts thus separated were for a time subject to the will of the parent animal, and in that respect were mere members of its body; but, when about to separate themselves from the rest of the system, they acquire a more intimate relation to each other, become actuated by a distinct will, and have, as it were, their own proper centre of action, even while they form part of the body of the parent worm. At length they become detached, and display free voluntary motion. The young individual thus produced consists at first of few constituent parts or members; grows, however, by the appropriation of new matter, and forms another compound system capable of dividing spontaneously, or of being divided, into several portions, "potentially" endowed with individual life. For a time this multiple individual is subject to the influence of a single will, and is only so far a multiple animal as the parts which compose it have the capability of becoming independent individuals, which as yet they are not "de facto." Subsequently, the individual parts, though still connected, are actual independent beings. Many Annelida and Entozoa may, indeed, be divided artificially into several distinct individuals, and are, therefore, not really simple animals, but systems of parts, each of which, however small its size, contains all that is essential to the idea of an independent organism, and has the power of producing an organism of the same species. The young Nais proboscidea is composed of fourteen segments only. During its growth an increase of these segments takes place at the caudal extremity, and, after a time, a part of the new segments begins to be separated by a constriction from the rest of the worm. Long before division takes place, however, new segments are formed by the parent animal at the constricted part; these new segments in their turn begin to be cut off from the body of the old worm, while others are produced above them. In this way we have sometimes presented to our observation a parent worm with three young ones, still forming part of one system which has itself been developed from a separated part of a former system.* (See fig. 145.)

When a Nais has in the process of growth thus multiplied its organism, the portions capable of separating from the parent animal, and of becoming separate individuals, already have the form of a young Nais; there being a repetition in the multiple animal of certain segments which the young and simple animal possesses only in small number. But an animal may in form present none of the characters of a multiple of individuals, and yet be constituted of a number of parts capable of becoming inde-

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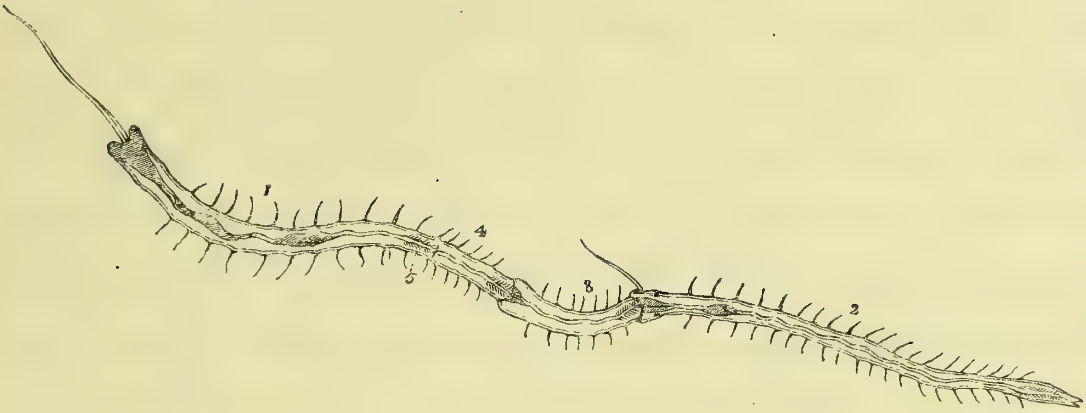
* O. Fr. Müller, Naturgeschichte einiger Wurmarten des Süssen und Salzigen Wassers. Copenhagen, 1800. See also Gruithuisen, Nov. Act. Nat. cur. xi.

Fig. 145.*



pendent beings. To this category belongs the Hydra, at the time when it is a simple polype animated by one will and destitute of sprouts. In this state, indeed, the polype is not a multiple of independent individuals, but it is really a multiple of all that is necessary for the development of a polype; for portions of its body, separated artificially, rapidly grow, and acquire the form of perfect animals, arms being protruded, and a digestive cavity developed within them. The experiments of Trembley, indeed, have shown it to be a matter of indifference whether the Hydra be divided longitudinally or into transverse ring-shaped segments, or whether portions are merely cut out of its side; the separated fragments being in all cases transformed into perfect polypes.† It would appear, therefore, that aliquot portions of the body of a polype, the limits of which are undefined, contain, like the leaves of plants, all that is essential to an individual of the species, and when no longer subject to the system of several such parts, united in the form of a simple animal, manifest the formative property resident in them, and become perfect polypes. In this respect the Planariæ resemble the polypes. It is true they never undergo multiplication during their growth, so as to form a system of independent beings, each endued with a distinct will, but always remain with respect to their volition simple animals. They may, however, as Dugès has shown, be divided into eight or ten separate segments, each of which will manifest independent life; and in summer, within the space of four days, will assume the form of a perfect individual of the species.‡

---

* [Figure of the Nais proboscidea. 1. Body of the parent worm; 2, 3, and 4, three young worms in different stages of development; 5, part at which new segments are being formed. After O. Fr. Müller, Von Würmern des süssen und salzigen Wassers. Tab. i.]

† Trembley's Mémoires pour servir à l'histoire d'un genre de polypes d'eau douce. Leide, 1744.

‡ Froriep's Notizen. No. 501.

It must not be supposed that the Hydræ and Planariæ, more than other animals, are deficient in organisation,—in the possession of organs and tissues. The structure of the Planariæ is already known with tolerable accuracy, and although, notwithstanding the advances made in the anatomy of the Hydræ, there is still much to be desired with respect to them, yet we cannot doubt that they are as perfectly organised as other polypes. In polypes, generally, the different structures are known to be most definitely marked; their movements are effected by muscles as in other animals; the arrangement of these muscles as well as of the intestinal canal is known; and in the Actiniæ, and even in the compound polypiferous animals, the generative organs have been exactly described. Since, therefore, separated fragments of a Planaria or of a Hydra, and of the latter animal very small fragments, contain within themselves the power of forming an entire animal, it is evident that this formative power must reside in a mass of different structures, as muscular fibres, nervous fibres, &c., which in the body of the parent animal were subservient to special functions of its system, and were subject to the influence of its will. It follows from this fact, that an aggregate of animal tissues of different physiological properties may be animated with a force quite distinct from the specific endowments of the respective tissues. The properties of the tissues included in the separated portion of a Hydra are, for example, contractility of the muscular fibres, the influence which the nervous fibres exert upon the muscular fibres, and so on. These properties are dependent on the structure of the individual tissues, and on the state of the organic matter in them. The formative power, on the contrary, which actuates the whole mass, is identical with that force by which the parent polype was developed.

The cause which compels a particular portion of a Hydra or Planaria to the performance of a subordinate function, is the mutual reaction of its component organic matter with that of the entire organism, which is endowed with a centre of nervous action, or a brain. In this condition the primitive formative force of each part remains latent, and its organisation is subservient to the central influence of the organised polype. As soon, however, as the portion of organised matter of a Hydra or Planaria ceases to be in contact with the rest of the organism which has a centre of action, it becomes withdrawn from the influence of that centre; and then the tendency to individual organisation is manifested. In the process which ensues, the different tissues already formed within the separated mass probably lose their distinctive characters, and become all transformed into formative matter ("cytoblastema"), and germinal or formative cells: the elementary parts of the tissues of the new animal being subsequently produced by the transformation of those cells. For it is thus that the different tissues of the embryo are developed.

The same, or very nearly the same law, prevails in plants. As long as the leaf, organised as a special organ of the plant, is connected with the branch, its faculty of reproducing an entire individual of the same species is kept in a latent condition, in consequence of the mutual reaction of the leaf, as an organ of the plant, with the entire branch or plant itself. For, though not possessed, like the polype, of a central source of action, diffusing an influence through the whole organism, yet every plant is maintained as an united system by the co-ordinate mutual reaction of all its constituent parts. If this mutual reaction is arrested by the dissolution of continuity between the leaf and the stem, the organisation which the former received for a special purpose in the general economy becomes useless, and the latent power of reproduction manifests itself by the formation of a bud, or the germ of a perfect plant.

If this view is correct, a separated part of a plant, such as the leaf of an orange or lemon-tree, which, placed in the ground, would put forth buds, ought, when grafted on the parent plant, to become attached and remain a mere leaf. I am not aware that any experiments of this kind have been performed, and intend the remark only as hypothetical. The supposition is, however, in some measure justified, since similar experiments on the polype have succeeded. Trembley divided a polype (Hydra) transversely, then brought the two halves together again, and kept them carefully in contact. Before the close of the same day they had united, and on the next day the union was so perfect that a small worm, taken as food by the anterior portion, passed also into the inferior half. At first the line of union was marked by a constriction; but at the end of a fortnight this had quite disappeared, and on the tenth day after the operation this polype put forth sprouts or buds. Trembley succeeded, likewise, in causing the anterior and the posterior half of two different polypes to unite, and the polype thus produced likewise budded, and produced young polypes both above and below the line of union.* It is a very important circumstance in this experiment that the lower half, after being cut off, again united as a simple portion of the entire polype, the anterior half of which contained the centre of nervous influence; that it remained as such during the long period through which the observation was continued, and did not develop itself to an independent individual, as it unquestionably would have done, had it, instead of uniting with the anterior half of the polype, been permitted to remain unconnected, and not in contact with it.

A further circumstance of importance is the difference of plastic power which Trembley found to distinguish portions taken from different parts of the polype. Very small segments cut in the most various directions from the body or cephalic portion of a hydra, became converted into new polypes; each assumed the proper form, soon acquired a central influence over other parts of the body, and independent voluntary motion; whereas the arms, when separated from the body, manifested no reproductive power. In animals higher in the scale, namely, Insecta, Arachnida, Crustacea, and Salamandrina, entire organs, such as the extremities, the eyes, or the lower jaw, are reproduced when lost, and this is sufficient to prove that the organisms of these animals are not mere aggregates of their constituent parts, but still retain within themselves the power of restoring the perfection of the whole when entire organs are lost. In these animals, however, the separated parts or organs never are developed into entire new individuals, but for the most part resemble in that respect the arms of the hydra.

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* Trembley, op. cit. pp. 292, 293.

It must also be considered, that since in the higher animals all the elementary tissues are developed from cells, and since, during the process of growth the number of the elementary parts of the tissues is increased by the addition of new cells, a full-grown animal of the highest organisation is also a multiple of the original sum of constituent parts or elements. In a full-grown Nais these multiples of the original sum of constituent parts are arranged in a consecutive series, and may be expressed thus: $abc + abc + abc + abc$. In other animals in which the sums of the different constituent elements cannot be isolated, not being arranged distinctly in a consecutive series, the young animal may be expressed by abc, and the full-grown creature by $aaa\ bbb\ ccc$, or by $a^n\ b^n\ c^n$. The multiple of the cells composing the liver, for example, may be represented by a^n; that of the cells of the nervous system by b^n; and that of the cells of the muscular system by c^n. These aggregates cannot in the higher animals become new individuals. But even here the full-grown organism may be regarded as virtually a multiple of the germ, since in the process of growth it has become capable of the formation of germs. It is true, the concurrence of two sexes is in this case necessary for the development of the new germs. But both these sexes may reside in one individual, as in all hermaphrodite animals, where fecundation is effected either mutually by two individuals, or, by each singly, as in the Tæniæ. A solitary individual organism, which in the perfect state produces fruit, or, in other words, scatters germs capable of becoming by development new individuals, must contain within itself the power of multiplication; and in this point of view every full-grown individual even of the higher animals, is, with regard to the power of individual vitality, to be regarded as virtually a multiple of the primitive vital force, and more particularly of the germ.

The question here presents itself: how small a portion of an organic body may contain the force necessary for the reproduction of the species? In the higher animals which propagate only by sexual generation, this force resides only in the germs of the ova, which are large cells containing the "germinal vesicle," and its nucleus, or the "germinal spot" of Wagner; while all other parts of their body, however large or small, are destitute of the reproductive power. In those plants and animals which propagate their species by buds or sprouts, the germ consists of a mass of cells which may be produced at almost any part of the body of the parent. In some of the lower animals the same reproductive power is possessed by every aggregate of organic elementary parts, that is, of such elementary parts as were originally developed from similar cells, but which subsequently have acquired the form and properties of muscular and nervous fibres, and of fibres of cellular tissue, &c. In the lowest organic beings the power of producing new individuals is not merely manifested by separate portions of most parts of the body, but in some cases subdivision, even into the ultimate particles of the organism, does not destroy this power: isolated elementary particles are adequate to the propagation of the species. In plants, generally, all the tissues are produced from cells; but there are plants in which any single cell separated from the rest of the organism, suffices for the reproduction of the entire plant, if nutritive matter be supplied. We have examples of this in the filiform fungi, such as the fungus of mould and the vegetable product, which, according to the observations of Cagniard Latour and Schwann, forms the active part of yeast, and the growth of which in large quantity gives rise to the fermentation of saccharine liquors. This fungus of yeast consists of cells arranged in simple or branched threads; and it grows by some of the cells developing upon their free surface a small prominence which becomes a young cell. This young cell soon attains the perfect size, but has scarcely reached its full development before it, in its turn, begins to put forth a bud, which is the germ of the next cell. (See fig. 149, p. 1436.) Single cells of this kind also separate themselves from the threads of which they formed part, and still in the isolated state form new cells by the process of budding, and thus propagate their species. All this process takes place so rapidly, that its different steps may be watched by means of the microscope.* The same phenomena are presented by all the simple fungi. The dust-like powder of the fungus so destructive to silkworms, the muscardine, is composed of cells endowed with the power of reproducing plants of the same species; hence we may easily conceive that a single grain or cell of this powder, introduced into a brood of silk-worms, may cause their entire destruction.†

CHAPTER II.

OF THE MULTIPLICATIONS OF INDIVIDUALS BY THE DIVISION OF PERFECTLY DEVELOPED ORGANISMS.—FISSIPAROUS GENERATION.

Since organic beings in the fully developed condition are virtually multiples of the germ which produced them, they are capable of multiplication by mere division, without the formation of new germs. This fissiparous generation is observed in animals quite incapable of the development of buds or "gemmæ." It may be the result either of the artificial interruption of contact and organic reaction between the different parts of an organic body, or of spontaneous division. In either case the separation may be complete, or only incomplete. When it is incomplete, the organic being appears as a compound or multiple system, the independent individuals of which are still connected by a common stem.

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* Poggendorf's Analen, xli. p. 184.

† See Audouin, Annal. des Scienc. Nat. 1837.

1. *Artificial fissiparous generation.*

The increase of organic beings by spontaneous division, which occurs for the most part only in the animal kingdom, is a less easy process than the multiplication by artificial division. Artificial division produces absolute interruption of continuity between parts which have already undergone perfect organisation, and at the same time are equally endowed with vital force; and it thereby causes the force resident in each part to assume an active state, so as to produce a new organism. Polypes, therefore, may be divided in any direction, and the separated portions will develop new individuals. While, on the contrary, spontaneous division always takes place in certain determinate directions, in which it is productive of the least disturbance of the internal organisation.

Multiplication of all plants, and of many of the lower animals, may be effected by artificial division. Branches, twigs, or sprouts, separated from a tree, are organisms which continue to live and maintain the species, when they are either planted in the ground or engrafted upon another plant. These cannot, however, be properly adduced as examples of true multiplication by division, effected independently of previously formed buds; for cuttings of plants are generally provided with fully-formed leaf-buds. It is true, a portion of a stem, deprived of its branches, and presenting on its surface no appearance of buds, will grow when planted. De Candolle, indeed, states that grafting will succeed when portions of bark, apparently containing no buds, are employed. Meyen, however, remarks,* with respect to this experiment, that adventitious buds formed in the medulla of the stock might force their way through the engrafted bark; and adds, that even a willow twig, stripped of its bark and used as a rose stock, put forth new sprouts after the lapse of several weeks, probably in consequence of the development of adventitious buds in the medulla or pith. Moreover, the growth of separated leaves, when placed in the ground, cannot in all cases be regarded as proving the possibility of multiplication by division without the formation of buds. When leaves of Bryophyllum calycinum, for example, are planted, they grow by the evolution of the buds which already exist in the axillæ of the marginal dentations. Even the cases in which leaves of perennial plants, destitute of buds and quite incapable of developing them while attached to the parent stem, strike root in the ground and send up stem and leaves, are not conclusive ; for, here the whole leaf is not transformed into the growing plant as the fragment of a hydra is transformed into a new polype, but develops a bud by its own vital power. This leaf, therefore, since it has the power of forming a bud, has itself individual life, and is already a simple plant. Leaves which thus grow when placed in the ground, are described by Meyen as sending out first the root and then the bud. The multiplication of lichens by artificial division is to be explained in the same manner.

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* Pflanzen-physiologie, b. iii. p. 84.

Multiplication by artificial division in animals is most likely to be successful when the organism consists of a succession of parts of similar structure, the number of which increases during growth. Annelida and Entozoa, for example, have this conformation, and transverse sections divide them into segments, each of which still contains similar though shortened portions of the nervous system, bloodvessels and intestinal canal. But this condition, although it facilitates the artificial fissiparous generation, is, as has been already mentioned, not absolutely indispensable. For in the multiplication of Hydræ and Planariæ by artificial division, the body of the animal may be cut in any direction, and each of the resulting fragments, though certainly not containing the essential parts of the organism, merely shortened, has the power of reproducing the individual. The property of producing a new organism of the same species is, therefore, possessed by any mass of elementary particles of the animal's body. Experiments have shown that there are three modes in which artificial division may be successfully performed.

1. *Transverse division.* It is principally when the organism has a linear and parallel development, consequently in plants and worms (Annulata, or Annelida, and Entozoa), that multiplication of the individual may be effected in this manner. But if the same worms, in which this mode of division succeeds, are divided longitudinally, the lateral halves do not live and develop new individuals. The transverse division succeeds very easily, as O. Fr. Müller showed in the naides. Hence Ehrenberg separates these worms, under the name of Somatotoma, from the Annulata. In other genera of the Annelida, though the separated parts of the animal after transverse division live for a long period, no reproduction seems to take place. The posterior third of a Nereis was kept by O. Fr. Müller alive, and possessed of voluntary motion, for three months; but it underwent no further development. Bonnet, however, states, that having cut a common earthworm in two, he obtained two perfect individuals. When, in Müller's experiments, a nais proboscidea had been divided transversely, the posterior half acquired in from three to four days a new head and proboscis. The division and decapitation of the parent worm seemed, also, to have no perceptible

influence on the spontaneous development of a young animal from the posterior part of the headless portion; and sometimes the head of this new creature, formed by spontaneous division, was developed as quickly as the head of the decapitated parent worm. During the warm season the hinder portion of a Hydra which has been cut into several portions acquires a new head and arms, in the course of twenty-four hours; and in two days it takes food. The process of reproduction occupies fifteen or twenty days in cold weather. Small segments of a Hydra have the same property.

2. *Longitudinal division.*—When Hydræ are divided longitudinally, the cut edges quickly apply themselves one to another so as again to form a tube; and, within so short a space of time as an hour, the external figure of the polype was seen by Trembley to be entirely restored, with the exception of the arms, which also were reproduced in a few days. A polype thus divided took food three hours after the operation. Bands cut longitudinally from a Hydra likewise quickly reproduce entire polypes. The artificial division of the trunks of vegetables in the longitudinal direction comes under the same head.

3. *Division in all directions indifferently.* — It is principally in the inferior plants, for example the lichens, and in the Hydra amongst animals, that the fragments resulting from the division of the individual in the most various directions have the reproductive power. Trembley having laid open Hydræ from one extremity to the other, cut them into several portions in the most various directions, and found that each portion became a perfect polype. If the portions into which the Hydra is divided are of such form that their borders cannot unite to form a tube,—if, for example, they be very narrow bands,—the digestive canal of the new polype is formed by the development of a cavity in the substance of the separated fragment. Imperfect division of a polype produces a Hydra with two or more heads, or a fasciculus of polypes united by their substance, though endowed with independent centres of organic and animal life. By partially dividing a polype in the longitudinal direction, from the head towards the tail, Trembley produced polypes with from two to seven heads. By laying open a polype longitudinally, and then cutting it in different directions, but so as not entirely to separate any portion, he produced a compound animal with several heads and several tails: each of the portions into which the polype was imperfectly divided being converted into the head or the tail of a new being, which still remained connected with the rest of the divided body.

2. *Natural or spontaneous fissiparous generation.*

Spontaneous division takes place, for the most part, either transversely or longitudinally, or in both directions at the same time. It is only in animals that this mode of generation occurs to any extent, and hence it has been employed, together with other characters, by Ehrenberg as a means of determining in doubtful cases whether simple organic beings belonged to the animal or to the vegetable kingdom. Fissiparous generation is a very common mode of multiplication amongst the Infusoria, though they also propagate by ova. Sometimes the gemmiparous mode of generation also is observed in the same genera. The higher animals never multiply by spontaneous division; and even the Rotatoria present no instance of it, though it occurs again in the Annelida. The complexity of the process must be greater in proportion as the organisation of the animal is more complex, and as there is less repetition of similar organs in its different parts. The non-symmetrical arrangement of organs on the two sides of the body does not, however, absolutely preclude the possibility of multiplication by spontaneous division, for animals which have a convoluted intestinal canal, as in the Vorticellinæ, propagate in this manner. In these cases there is [no ?] reason to think the division owing to the masked development of a bud, for the perfectly organised animal is seen to become divided in the longitudinal or transverse direction by a gradually increasing constriction. The cause of the spontaneous division is the striving of the organism, rendered virtually a multiple by the process of growth, to concentrate the sway of the organic force upon smaller masses. In proportion as the size of the system, as yet under the rule of one centre, increases, in the same degree do the organic particles which compose it seem to lose their attraction for this common centre, and gain a mutual attraction for each other in smaller groups, which then form independent centres. The plants which present the phenomenon of fissiparous generation are the Palmellæ, in which it has been observed by Morren.

The observations of Ehrenberg* show that the mode of generation by spontaneous division prevails much more extensively amongst the Infusoria than in other organic beings. The monads propagate their species by transverse and longitudinal division; and even those which are furnished with a shell are not exempt from this mode of multiplication. The Volvocinæ undergo division in the interior of their envelope, which afterwards bursts; the young animals resulting from the division being then set free, to undergo in their turn the same process. The Baccillariæ divide spontaneously in the longitudinal direction, and, their division being imperfect, form for a time compound, chain-like bodies. Some, as the Gomphonema, are, after their longitudinal division, able to detach themselves entirely from the stem by which they at first remain connected. The Vorticellæ divide in the longitudinal direction, and

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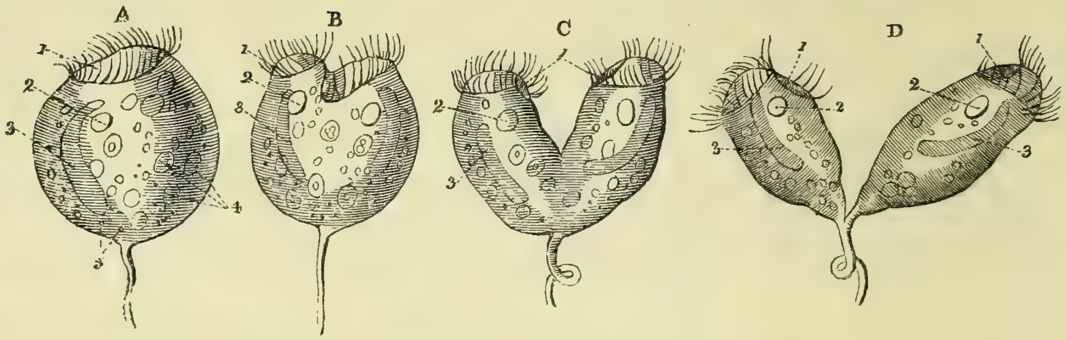
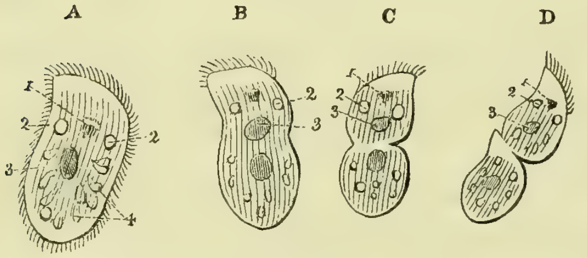
* Die Infusions-thierchen, als Volkommene Organismen. Leipz. 1838.

Fig. 146.*



then set themselves free from their common stem (see fig. 146). The families of Enchelia, Trachelina, Colpoda, and Oxytrichina also multiply by longitudinal and transverse division (see fig. 147).

Fig. 147.†



The results of the observations of O. Fr. Müller and Gruithuisen, upon the generation of the naides by spontaneous division, have been already related. After a constriction has shown itself, marking the point of separation between the body of the parent worm and its posterior part, which is to be developed into a new individual, but long before the separation is effected, a head and proboscis is formed upon the latter at its anterior extremity, and the part immediately in front of this begins in its turn to be separated from the parent worm; so that sometimes a nais is seen with three young individuals still connected with it (see fig. 145, p. 1425). Fissiparous generation is also observed among the Planariæ.

The spontaneous division of animals is generally complete, but sometimes it is incomplete. Monads, which undergo imperfect division in the longitudinal and transverse directions alternately, form bodies like clusters of berries. Successive divisions in the longitudinal direction give rise to series of individuals united by their lateral borders. Repeated imperfect division in the transverse direction produces linear series of individuals. Of the latter nature Ehrenberg regards the Vibriones, which often are observed to consist of two or three, or very many articulated portions, remarkable for their quivering motion. The ramified Vorticellinæ,—Carchesium and Epistylis of Ehrenberg,—are produced by imperfect dichotomous division, the resulting halves remaining attached to each other by the stem prolonged from their posterior extremity. This mode of division is observed, though only in few cases, among the Polypifera; it occurs, according to Ehrenberg, in the Caryophyllæi, and gives rise to their dichotomous, tufted, and pedicillate forms, two polypes being produced from one, four from two, eight from four, sixteen from eight, and so on.

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* [Vorticella microstoma multiplying by spontaneous longitudinal division. The figures A, B, C, D, show successive stages of the process. 1, mouth; 3, sexual gland; 2, contractile sac; 5, ova; 4, gastric sacs. After Ehrenberg, Infusionsthierchen, taf. xxv.]

† [A polygastric animalcule, Chilodon uncinatus, multiplying by spontaneous transverse division. The figures A, B, C, D, show successive stages of the process. 1, mouth, surrounded by a fasciculus of bristles or teeth; 2, contractile sac; 3, sexual gland; 4, stomachs. After Ehrenberg, Infusions-thierchen, taf. xxxvi.]

The occurrence of spontaneous division in the vegetable kingdom, is still subject of dispute. Ehrenberg* declares that no plant with which he is acquainted, no part of a plant, nor even a cell of any plant, undergoes multiplication by spontaneous division. The only modes of increase in plants, according to his view, are elongation and the formation of buds; the cases of apparent division depending merely on the separations of buds or gemmules. Meyen,† on the contrary, maintains the frequent occurrence of this mode of increase in the case both of entire plants and of the cells of plants. Meyen founds his opinion partly upon the genus Closterium, which Ehrenberg, on the other hand, refers with several other organic beings difficult of examination, but all multiplying by spontaneous division, to the animal kingdom. The other instances adduced by Meyen seem to me to be examples of the formation of spora by division, and of the separation of individual cells. There are, however, vegetables of such simple structure that they consist of a mere filiform tube; and here spores are formed by the mere constriction, and, in fact, division of this tube; the spores being the "simpla" of a virtual "multiplum." There are other structures in which the cells produced as buds from the parent cell, and forming a connected chain, constitute the "multiplum" of the plant, which then separates into its "simpla" by true division. Meyen adduces observations on Palmellæ, Oscillatoriæ, Nostochinæ, and filiform Fungi. The spherical coloured mass which constitutes an individual of the genus Palmella, is always included in a coating of mucous matter within which, as the parent cell, the spontaneous division of the coloured mass takes place. After its division is effected, each portion of the mass comes to be invested by its proper mucous coat, and at the same time the external common vesicle of mucous matter is absorbed, though sometimes before its absorption it expands considerably, so that the new individuals, with their fully-formed proper investments of mucus, can be seen free in its interior. The green mass in the simple tube of the true oscillatoriæ was seen by Meyen to be at first undivided, but to become subse-

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* Bericht über die zur Bekanntmachung geeigneten Verhandlungen der K. Pr. Academie der Wissenschaften, 1836, p. 34.

† Neues System der Pflanzen-physiologie, b. iii. p. 440.

quently split into several masses. Sometimes the green matter became divided into a greater or less number of long segments, and then the tube separated into portions corresponding to these segments. Here the spontaneous division appears to me to consist in division of the spore-mass. The bead-like threads which in the genus Nostoc lie in a gelatinous mass (the phycomater) increase in length, according to Meyen, by the spontaneous division of their component vesicles or cells. When the old Nostoc perishes, those cells escape from the gelatiniform mass, each having the power within itself of enlarging and becoming a new Nostoc. The spores of the Nostoc consist of a greenish and somewhat hardened gelatiniform substance, and are filled with a mucous colourless fluid; during the formation of the new plant, the coloured wall of the spore swells and becomes the gelatinous mass of the Nostoc, while in the contained fluid there appear opacities which produce the first vesicles. These vesicles subsequently undergo repeated spontaneous division, and thus become the bead-like spore-threads. The moss and liverwort tribes also, according to Meyen, do not form their seeds within parent cells, but produce them by division, and the individual seeds are first separated by constriction from the larger parent seed. Meyen regards the increase of the cells of some articulated confervæ, for example, Conferva glomerata, by the protrusion of a part of their walls, and the subsequent separation of the protruded part by a constriction, as an example of the same process. In the lower fungi, as the Penicillium glaucum, also, the development of the sporules is effected, according to Meyen, by the division of the thread-like tube (see fig. 148). In the fungus of yeast, Saccharomyces, which consists of a string of cells, each new cell is formed as a bud from the extremity or side of an old cell (see fig. 149). The component cells of the fungus readily separate from each other, and, when isolated, bud again, and produce new systems of cells. Each cell of the plant is here a spore, or is an individual, which undergoes multiplication by the process of budding, while the newly-formed individuals readily separate themselves

Fig. 148.*

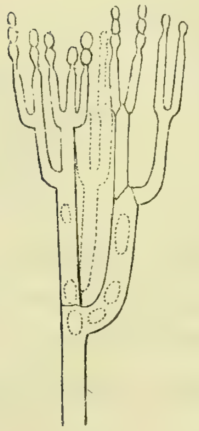
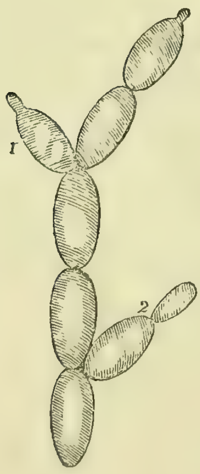


Fig. 149.†



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* [Figure of Penicillium glaucum, showing the development of spores by division of the tubular cells. After Meyen, Pflanzen-physiologie, tab. x. fig. 20.]

† [Figure of the fungus of yeast, Saccharomyces cerevisiæ. 1, a cell, developing a bud from its extremity; 2, a bud becoming separated from the parent cell. After Meyen, op. cit. tab. x. fig. 22.]

from the systems of which they first form part. The spontaneous division of the fungus of yeast consists, therefore, in the separation from each other of individuals originally produced by the process of budding,—the gemmiparous process. It is very analogous to the separation of the young polypes which bud from the body of the fully-developed parent polype; in other words, to the resolution of a compound system of perfect polypes, produced by the development of buds, into separate independent individuals.

CHAPTER III.

OF THE PROPAGATION OF THE SPECIES BY BUDS.

The formation of buds is essentially due to the following process:— A portion of the substance of an organised being, superfluous for its individual life, separates itself in an undeveloped state of organisation from the organism of that being, so far as to assume a special individuality of life, without, however, losing its organic connection. From the germ thus produced the special organisation of the species is subsequently developed in the form of a new individual, which may either retain its organic connection with the parent trunk or become detached. This production, by one living individual, of the germ of a new living individual, presupposes that the parent trunk already contained within itself the organic force for several beings, and was, in fact, a virtual "multiplum." The process of the formation of buds, though a variety of imperfect spontaneous division, differs from the true fissiparous mode of generation. For, in the latter process, the perfectly developed organism divides into two, or more, perfectly organised segments. Here, therefore, the entire production of a special structure in the separated parts is not required, since the special organisation already exists, and only needs such changes as will restore to integrity the parts involved by the line of division; while, in the process of the formation of buds, the new individual represented by the bud is not perfectly organised, but is merely endowed with the power of developing a perfect organism. The bud of a plant is, therefore, to use the words of C. Fr. Wolff, the "simple plant," and the bud put forth by an animal, the "simple animal." A bud originally consists merely of the primary elements of all organisation, namely, cells, and contains even these in proportionally small number. The buds of plants are masses of ordinary vegetable cells. The vessels of the parent plant have not the least share in the formation of the original bud, and have no connection with it until a later period. The bud appears in fact originally to be a mere prolongation of the cellular tissue of the pith, as Duhamel, Treviranus, Meyen, and others state. It is not separated from the pith of the mother plant by any septum; merely cells of smaller size being interposed between them.* Usually the buds of plants are developed upon the parent stock, but sometimes they fall off and are developed separately, as in the cases of some monocotyledonous and dicotyledonous plants and the Hepaticæ.

The ovum is distinguished from the bud, not only by the circumstance of sexual influence being necessary for its development, but also by its inability to undergo further evolution while forming part of the parent organism, and by its being insulated from the parent plant by distinct membranes. The spores, developed independently of sexual intercourse by many of the more simple plants, cannot be regarded as germs of ova.

The causes which determine the development of buds in the parent plant are partly internal and partly external. The more simple organisms form a substance which has the power of developing new individuals with the proper organisation of the species. When this substance does not receive a special structure adapted for the performance of some function of the existing individual, and therefore is not subjected to the proper vital force of this individual, it exerts its power of independent organisation, and forms a new individual. The limits of this individual are determined by the larger or smaller size of the mass of elementary parts (cells), which thus become connected by a special mutual reaction, while they are excluded from an equally intimate reaction with the parent organism, and are also separated mechanically in some way or other, by a heterogeneous substance, from other masses of substance capable of forming buds. Wherever, therefore, in an organic body substance is formed which the organism does not require for the constitution of special structures, and does not retain under its central influence, there buds are formed. The formation of this substance seems explicable by the same supposition as that which was proposed to account for spontaneous multiplication by division; namely, that the organism being a virtual "multiplum," and increasing by growth, strives to concentrate its organising force upon smaller masses.

Another cause determining the formation of buds in plants is an intermission of the activity of the vital force of the individual in the production of special structures from the organic matter, or an intermission in the general nutritive function. In many plants the formation of buds takes place only at the periods when the exterior growth ceases for a time, and when the leaves have fallen off. Hence it is, also, that plants may be most successfully transplanted when they are destitute of leaves. On the contrary, the more the juices of a plant are expended in the multiplication of the elementary tissues and organs, the less capability is there for producing compound "multipla," which are composed neither of *a*, nor of *b*, nor of *c* alone, but have the properties of *a, b, c*, &c. united.

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* See Treviranus, Physiologie der Gewächse, b. ii. p. 630.

Any circumstance which arrests the general growth of the organism at any point, or only interrupts the continuity of the cellular tissue, may determine the formation of buds in plants. Hence buds are produced at the margin of fleshy leaves when they have been subjected to moderate pressure, and also in wounds of the bark.*

1. *Of the formation of "buds" or "gemmæ" in plants.*

a. Buds of the inferior or non-vascular plants.—The buds of the plants of low organisation consist partly of aggregates of cells, partly of single cells. In the moss and liverwort tribes they are of the former kind. Those of the articulated Confervæ and filiform Fungi, on the contrary, are single cells, which are either portions cut off by gradual constriction from the parent cell, or tube, (gemmation by spontaneous division,) or are produced by the protrusion of the wall of the parent cell, and the subsequent separation of the protruded portion as a distinct cell, by the process of constriction. Buds of this kind are formed in the way first-mentioned in the filiform Fungi, such as the Penicillium glaucum (in fig. 148, p. 1436); in the latter mode in the articulated Confervæ, such as Conferva glomerata, and in the fungus of yeast (see fig. 149, p. 1436). There is no essential difference in the two processes.

b. Buds of the more highly organised vascular plants. — Axillary and Terminal buds. — The buds (leaf-buds) of the higher plants are either formed in the axes of leaves, or at the extremity of the stalk or stem. The leaf-like structures which sometimes appear as scales enveloping the apex of the axis of the bud or the embryonic nucleus of the future axis, may be absent, in which case the nucleus of the bud is naked. This body is formed of cells which, by spontaneous development, become the new sprout. The cellular pith of the stem of the plant is continuous with the cellular nucleus of the axillary and terminal buds. The development of the special organisation of the plants from the cells of the existing buds is always attended with the formation of new buds for the next period of vegetation.† In the production of the special structure of the species, therefore, something in addition is always generated, which does not form a component element of the present organism, but contains the organic force for future vegetation.

In phanerogamic herbs the buds are sometimes naked, sometimes covered with scales. The simplest buds are in these plants mere masses of cells. In the Lemna the bud issues from the cleft of the parenchyma in the form of a small leaf which subsequently becomes a new plant; but even before its escape from the cleft it possesses a root folded up within it.*

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* Treviranus, Op. cit. pp. 625, 626.

† See Meyen, Pflanzen-physiologie, b. iii. pp. 5. 7.

The buds of trees, on the contrary, are composed of enveloping scales and included parts. The structure of such buds is described by Treviranus † as follows: — The bud itself appears between its coverings (tegmenta) as an elongated or roundish cellular body, the groundwork of the future leaves. At the point where a bud is to be formed the pith or medulla of the stalk undergoes enlargement, and dilates the surrounding woody mass. The pith, which was hitherto colourless, develops now a dark green cone of small-celled tissue, surrounded by a sheath which, in a transverse section, appears as a delicate line. This sheath of the cone is formed of the innermost layer of wood, and the liber, which meet at the margin of the woody mass. The sheath thus formed is not closed at the inner extremity of the cone, where the bud rests upon, and where it consequently communicates directly with, the pith of the stem. The colourless inner bark of the twig or branch is continued over the outer side of this sheath, and forms the scales of the bud, while the external green bark ceases at the base of the outermost scales. As soon as the transformation of the bud into a branch commences, spiral vessels are developed. Inferiorly these vessels apply themselves to the woody mass of the stem, while in the opposite direction they follow in their development the extension of the bud. Lastly, they form the commencement of a new layer of wood, which belongs in common to the new twig, and to the axis from which it springs. In the twig this new layer of wood has the first place next to the pith; in the larger branch it has the second place. Flower-buds are distinguished from leaf-buds by the circumstance that they can produce no further generation of buds except by sexual fecundation. When fecundated they resemble the deciduous leaf-buds. In rare cases, however, an unimpregnated flower-bud becomes developed into a branch. Thus, according to Meyen, the nucleus of the unimpregnated ovum of Poa (a genus of the grass-tribe) grows and becomes a new individual; the development of which, however, remains imperfect. (These are the so-called viviparous plants.)

Adventitious leaf-buds.—Buds which are neither axillary nor terminal, but which make their appearance through the bark of the old stems and branches of trees, are thus named. They are connected with the medullary rays, and through their medium with the cellular pith, which reaches the surface at all points of the stem and branches, and thereby renders possible the formation of adventitious buds at all points. Adventitious buds are sometimes developed in extraordinary number on the stems of trees which are no longer able to vegetate by the axillary and terminal buds, in consequence of both the axillæ of leaves and the terminal axes having been cut away.

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* Treviranus, Physiologie der Gewächse, b. ii. p. 631.

† Op. cit. b. ii. p. 632; b. i. p. 258.

Buds on leaves.—There are many plants also, in which buds are developed, either normally or under the influence of particular circumstances, on their leaves. The best known instance of this is afforded by Bryophyllum calycinum, where the buds are seated in the notches of the margin of the leaves, forming there conical knots. These buds sometimes undergo further development while still upon the plant; but they do so more readily after the leaves have fallen off. Leaf-buds of this kind are met with in many ferns, and, among the higher organised plants, in Malaxis paludosa, Cardamine pratensis, and the genus Lemna.

Tubers.—These are subterraneous stems with unusual development of the cellular pith and cortical portion, between which the vessels are placed. Buds develop themselves in this tuberous portion of the stem just as they do in the aërial stem. Since the original stem in annual tuberous plants dies every year, the portion of the stem in which the tubers are developed seems destined for the continuance of the species. The subterraneous stems, on which the tubers are destined to be formed, are developed while the plants are quite young, as offsets, which have the same structure as the aërial stem. When the tubers begin to be formed these shoots enlarge at one or more places, in consequence, partly, of the increase of the medullary substance, and, partly, of thickening of the cortical portion. The spiral vessels consequently lie between two inordinately developed cellular masses, the cells of which contain granules of starch. At first the tubers are but small, so that the spiral vessels are not much separated from each other; but with the increase of the tuber they become more spread asunder. A tuber may form at any part of a subterraneous stem. The axis or nucleus of the bud is here, as elsewhere, a prolongation of the medulla; it is, namely, a conical body produced from the surface of the medullary mass, and accompanied by spiral vessels, which makes its way through the cortical portion of the tuber, and appears at the surface seated in a depression. The buds for the succeeding periods of vegetation are visible even in young tubers of the size of a pea.*

Bulbs.—Bulbs, according to Treviranus, are buds, the scales of which have become fleshy or succulent. They are developed at the side of the base of the stem, and remain for a time connected with it by cellular tissue and vessels; in consequence of the desiccation of this bond of connection, however, they at length become free. Bulbs may form on the aërial as well as on the subterraneous stem. Bulbilli of the aërial stem occur in the genera Lilium, Allium, Saxifraga, Dentaria, and many others, where they are developed in the axillæ of the leaves or of the floral envelopes. When the axis or nucleus of these bulbs begins to be developed into the new plant, it derives nutriment from the fleshy leaves.

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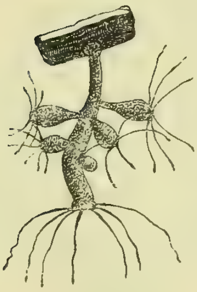
* Meyen, op. cit. b. iii. p. 26—31.

2. *Of the gemmiparous generation of animals.*

In the animal kingdom, the propagation by the formation of gemmæ or buds is met with to the greatest extent in the class Polypifera, and less frequently in the Infusoria; for example, in the Vorticellinæ. Sars observed its occurrence in Cytais and other of the Acalephæ. Of the Entozoa the order Cystica alone presents examples of this mode of propagation. In Cœnurus, the vesicles which bear the numerous heads are at the same time germ-stocks, upon which the new individuals are developed as buds. In Echinococcus, the parent animals take the form of vesicles, on the inner or outer surface of which new individuals are developed, and to which they are for a time connected by a thin filament; but, subsequently, the young ones become free.* Hence the old Echinococci have the form of vesicles containing other vesicles, and have been incorrectly called acephalocysts.

The more intimate steps of the process by which buds are developed in animals have not been observed, nor has any satisfactory microscopic examination of the structure of an animal gemma ever been made. The facts, however, with which we are acquainted relative to the development of the animal tissues, place it beyond doubt, that the buds developed by animals, like those of plants, are at first mere masses of cells, and that these cells not merely increase in number but undergo a special arrangement and transformation so as to produce the different tissues of the body. In the Hydra the gemmæ appear first as small roundish prominences upon the surface of the cylindrical body of the animal, at any point of which, except the arms, they may form. These gemmæ soon acquire the proper form of the polype (see fig. 150); but at first, as Trembley has shown, the cavity of the young polype is continuous with that of the parent hydra.

Fig. 150.†



In the Sertulariæ the gemma is at first an obtuse projection from the stem, closed at its extremity, but containing a cavity which communi-

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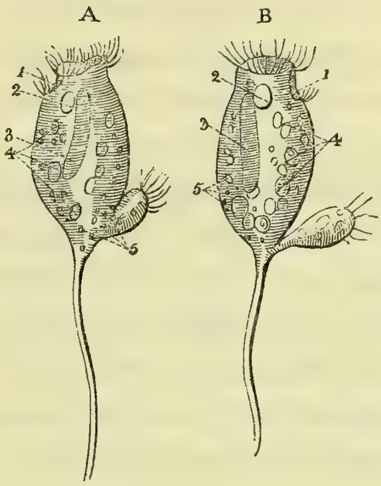
* See J. Müller, in Müller's Archiv. 1836. Jahresb. CVII. Von Siebold in Burdach's Physiologie, b. ii. 2te Auflage.

† [Figure of a hydra, from which several young ones are being developed; at first in the form of round buds. The parent polype has just taken a worm, and a part of the food has passed into the cavity of each of the young ones. Trembley, Mém. pour l'Hist. des Polypes. Planche, viii. fig. 7.]

cates with the canal of the stem. Subsequently the organisation of the polype takes place, and then the extremity of the gemma opens and the arms of the polype are put forth.* The formation of gemmæ is very frequent amongst the Polypifera, but less so amongst the Infusoria. Spallanzani and Ehrenberg have observed it in the Vorticellinæ (see fig. 151). Perhaps the naides should be regarded as multiplying by the formation of buds. For since the young individuals are formed from the hinder part of the parent animal (see fig. 145, p. 1425), and since at this part new segments are constantly being formed, it is possible that the young organisms which separate from the parent body are merely gemmæ which have undergone development, and consequently that the apparent spontaneous division of the parent body is really a throwing off of terminal buds developed upon the parent stem.

Fig. 151.†



The compound polypiferous animals increase by the production of gemmæ, which do not separate from the parent stock, and thus give rise to a constantly extending mass, which includes successive generations of united individuals. In many animals,—as the Ascidiæ, Xeninæ, Sertularinæ, and Alcyonellæ, the gemmæ are formed upon stoles or running stems.‡ We have seen that in plants, after the terminal and lateral branches are cut away, the stem will produce buds. A similar fact is observed with respect to the polypifera: sometimes, when all the individual polypes have perished, the formation of buds upon the stem will continue.

CHAPTER IV.

OF THE SEPARATION OF THE BUDS OR GEMMÆ, OR OF THE DIVISION BETWEEN THE STEM AND BUD.

Buds may separate spontaneously or be detached artificially, so as to become perfectly independent individuals, either in their simple state or when they have already by development acquired the organisation proper to the species. All these varieties of the phenomenon may occur in animals as well as in plants.

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* Lister, in Philos. Transact. 1834, Pt. ii. [Also Farre, Philos. Transact. 1837.]

† [Vorticella microstoma multiplying by gemmation. A and B show successive stages in the development and separation of the young animal. 1, mouth ; 2, contractile sac ; 3, sexual gland ; 4, stomach ; 5, ova. After Ehrenberg, Infusionsthierchen, t. xxv.]

‡ See Ehrenberg, in Bericht über die Verhandl. der Akad. der Wissensch. *Zu* Berlin, 1836.

a. Artificial separation of gemmæ which have undergone development.—Gemmæ of the Hydra which have acquired the proper form of the polype live when separated artificially from the parent animal. This mere separation of two perfect individuals must be distinguished from the artificial division of a single animal.

In plants, this separation of a fully-developed bud, or of a sprout, is very often performed, either for the purpose of planting it in the ground or of grafting it upon another stock. This, however, is not such a perfect example of the separation of individuals developed from buds, as are some cases observed in the animal kingdom; for the cuttings and scions of plants are usually not mere twigs calculated to vegetate by the extension of already existing parts, but sprouts which contain other buds ready to undergo development.

b. Artificial separation of buds which are still in the embryonic condition.—Of this an example is afforded us in the propagation of potatoes. For separate buds or eyes cut out of the old tuber, with a portion of cellular tissue surrounding them, vegetate when set in the ground.

Buds of plants separated while in this simple state will also grow when engrafted, together with a portion of bark and wood, upon other plants. No experiments of the same kind have been performed upon animals.

c. Spontaneous separation of buds which have undergone development.—The bud of a Hydra which has acquired the perfect organisation of a polype, and has long evinced by its movements its individuality and independence of action, at length separates itself spontaneously from the parent stock, the division being effected by gradual constriction at the point of their connection.

In the compound polypiferous animals the buds which have become developed into perfect individuals, remain, as in plants, connected with the perennial parent stock, which their successive generations aid in extending.

d. Spontaneous separation of simple embryonic buds.—The spontaneous separation of simple buds or gemmæ from the parent stock is very frequent in plants. The separation of the bud-like spores of the filiform fungi and mosses, of several of the liverwort tribe, and also of some ferns, are examples of its occurrence.

The formation of tubers and bulbs upon a parent stock, which may either perish annually or be persistent, also ends in their separation, together with the mass of nutriment with which they have been furnished by the subterraneous stem of the parent plant; and the aërial bulbs or "bulbilli" of the genera Dentaria, Saxifraga, &c. are likewise deciduous.

In animals, such deciduous buds or gemmæ seem to be rare. The existence in animals of a non-sexual mode of generation by means of spores, was formerly admitted in many cases, but the more accurate examination of the generative organs in those animals has rendered it probable that in many such cases the reproductive power of the apparent spores depends on sexual fecundation. It has hitherto been found impossible to establish an absolute line of distinction between the two kinds of germs even in plants, namely, in the Cryptogamia. Germs which are produced without sexual influence are essentially of the nature of buds or " gemmæ," whether they consist of single cells or of many.

Deciduous buds resemble very closely in their nature the germs of ova, that is germs rendered capable of development by sexual influence. In both the perfect organization of the plant or animal is wanting, and both are composed simply of one or more cells, which are endowed with the power of producing the entire organisation of the species. But, while in deciduous buds, spores, &c. the process of development requires no other conditions than the ordinary external vital stimuli, or general conditions of life, the germs of ova, on the contrary, are incapable of further development until they have been exposed to a "complementary" agency. Both the germ of the ovum and the semen possess the power of affecting the determinate organisation of the species, for the new individuals present peculiarities both of the male and of the female parent, but neither can exert its power until by reciprocal action with the other the deficiency in its endowment has been supplied. Buds and the bud-like spora are subject to no such condition. The fissiparous and gemmiparous modes of propagation differ from sexual generation, also, in the greater certainty with which they preserve the peculiarities of the individual. Hence, the method of planting cuttings, or that of grafting, is always preferred when it is desired to have all the properties of the parent stock in the new individual. The sexual mode of generation affords much more scope for variations, and can be trusted only for the propagation of the species, but with no certainty for the reproduction of the peculiarities of the individual.

The germs of ova, however, not unfrequently acquire the nature of buds or spores. Many observations have rendered it an established fact, that butterflies, kept perfectly isolated from the male insect, have laid eggs, from which young have been developed. Still better known is the fact pointed out by Bonnet, that the Aphis, though kept apart from the male insect, from the very time of its escape from the egg, nevertheless produces living young. In some rare instances, also, for example, in the genus Poa, as has been mentioned already, a new individual is developed from the unimpregnated flowers of plants, as from a bud. In these cases, therefore, the germ of the female acquires insensibly the nature of a bud; the defect in its reproductive power, which ordinarily renders the semen of the male necessary, being removed.

CHAPTER V.

THEORY OF NON-SEXUAL GENERATION.

The production of new organic beings from individuals already existing, may *à priori* be conceived to take place by either of the two following processes:—It may be the result of the entirely new formation of germs by the parent organism; or it may be effected by the mere unfolding or setting free of germs contained within the parent from the commencement of its existence. The latter view is the one adopted in the theory of "evolution," which has numbered amongst its supporters physiologists of the highest reputation, as Bonnet, Haller, and even Cuvier. According to this theory, the first created embryos of each species must contain within themselves, as it were, in miniature, all the individuals of that species which shall ever exist, and must contain them so arranged, that each generation should include not only the next, but, encased within it, all succeeding generations. Hence this theory has also received the appellation of the "emboitement" theory. The encased germs have at one time been supposed to exist in the ova, at another time in the spermatic animalcules.

Opposed to this theory is that of "Epigenesis," according to which, existing organisms do not contain the germs of future individuals, encased within them *ab initio;* but each new germ is an entirely new production of the parent organism. Casper Friedich Wolff was the celebrated and successful advocate of this view, which has been received by the best of modern naturalists. The "evolution" theory in its first crude form was completely refuted by Wolff* and Blumenbach.† For the germ certainly does not contain the miniature of the organic being in its perfect form, nor can such an opinion be any longer maintained. The germ of the embryo of vertebrata, in the earliest period of its development, presents not the slightest resemblance to its subsequent form. The various organs in the process of their development do not undergo a mere increase of size from a miniature condition, but we see them actually produced before our eyes. All the tissues of the body are formed from cells, and all the organs are composed of those tissues. In order, therefore, that the "evolution" theory should be tenable in the present state of science, it would be necessary to give it a more subtle form. There are two states in which the same organism exists at different periods, namely, that of the germ, in which it possesses the power of producing the proper organisation of the species, but has not yet assumed that organisation; and, again, the state in which its organisation is perfected, and in which it in part returns to its original state, and produces germs.

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* Theorie der Generation, Halle.

† Ueber den Bildungs-trieb, Göttingen, 1791.

Now, supporters of the evolution theory at the present day could only maintain, that the organisms of future generations are encased in the form of germs,—that the perfectly formed organism contains the next generation in the condition of germs or embryos, and these, again, the succeeding generations as other germs. Encased generations of individuals of this kind do exist; for example, in the polypes and naids; and even the human female, when pregnant, encloses one generation in the developed state, the fœtus, and in the ovaries of this fœtus the germs of a third generation, as ovula with their germinal vesicles. The eye, aided by the microscope, can detect no further encasement than that of the ova, germinal vesicles, and germinal spots; but still it might be maintained, that, though not discoverable by human vision and instruments, such further encasement may exist; and arguments of this kind are unanswerable. The problem may, however, be investigated in a simpler form than that in which it presents itself to us in sexual generation. We may leave out of consideration the mysteries of the latter process, and compare the theory of evolution with the facts of non-sexual generation. We have seen that an organic body may undergo multiplication by division, by the formation of buds, and even by the process of growth. We have stated, moreover, that the cells, which are the ultimate elements of organic bodies, multiply themselves partly by the formation of new cells in their interior or on their exterior, and partly by undergoing division, and by the separation of protruded diverticula. Lastly, there are organisms where each cell is a germ or embryo which produces the new germs of the species, by the protrusion of parts of its walls, and the subsequent separation of the protruded portions in the form of new cells.

These facts afford the most decided refutation of the evolution theory. A perfectly developed organism, which was shortly before governed by a single will, is divided, and immediately two wills are manifested. Such, at least, is undeniably the case when some worms are divided artificially; each half of the former individual moves itself independently. Again, in the spontaneous division of a perfectly developed organism two independent individuals are produced from one, in a manner which renders it certain that the multiplication is not due to the evolution of pre-existing encased germs. The evolution theory is also inapplicable to explain the gemmiparous mode of increase of the lowest plants, (as the articulated Confervæ and the fungus of yeast,) where a multiplum is produced by the division of a single cell, or where a cell protrudes a sacculus at one part of its walls, which at first is part of the old cell, but becoming separated from it by gradual constriction of its neck forms a new germ (see page 1436).

Since, therefore, the germs of organic bodies do not contain within them the seed of the next and all succeeding generations, and since they acquire the power of forming multipla in the process of growth and by the assimilation of surrounding matter; no other alternative seems to be left for us than to admit that the multiplication of all organisms takes place by division. The essential vital principle of organic beings either has the property of undergoing division *ad infinitum*, without losing its specific plastic power, or it is rendered capable of this division for the endowment of several organisms by the appropriation of foreign matter and the forces resident in that matter. In the latter case we must admit, either that the seed for all living beings exists in a latent state in the material world, and is extracted from it by productive individuals, or that the material world is animated by a force which, Proteus-like, can assume many forms, but which, having combined with matter so as to constitute a specific organism, is compelled by the form which it has assumed to certain specific actions.

An important step in the elucidation of the process of generation has recently been made in the discovery of the vital endowments of those elementary particles which the observations of Schwann, now well known and fully confirmed, have shown to compose both animals and plants in the embryonic state. All parts of plants and animals are developed from cells. The germ of animals, and of many plants, is a simple cell, and the essential part of the gemma or bud, is either an aggregate of cells, or a single cell. The embryo of plants and animals, also, when in the process of development, is composed of a number of cells similar to the first, or germ cell. In the lower plants,—for example, in the filiform Fungi,—any one of the component cells separated spontaneously or artificially from the aggregate of cells which form the plant, is adequate to the production of many similar cells. From these facts we may deduce two conclusions, which have been already noticed by Schwann,* and of which one or the other must be true, to the exclusion of any third view.

I. Since all tissues and organised parts are produced from cells similar to those which singly or in certain number compose the germ; since all cells within the growing organism by their influence on the surrounding nutrient matter can determine the formation of new cells either in their interior (as in the case of the cells of cartilage, and of the chorda dorsalis) or on their exterior (as in the case of the cells of epithelium); and since in the lowest plants each cell separated from the organism can become a new organism, and in some simple animals, as the Hydra, a fragment separated from their body has power to develop an entire new individual; since, lastly, the elementary tissues composing such a fragment of a polype, whatever their form and nature, whether muscular fibres or nervous fibres, are all modifications of cells, it is concluded not merely that an organic being may be constituted by a single cell; but that every perfectly developed organism is a mass of cells, or of parts developed from cells, each of which has the power of developing an entire new organism.* This view is evidently correct with regard to certain organic beings, such as the filiform Fungi, and to a certain extent, even in the case of the Hydra; but it is not proved to be applicable to all organic beings. Let us, however, for a moment suppose its universal tenability, and inquire to what further inferences it would lead.

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* Mikroskopische Untersuchungen, p. 220.

If every component cell of an entire organism, and even the product of cells possesses the power of reproducing the entire individual, by the formation of new cells, by their aggregation in definite forms, and by their transformation according to the necessities of special functions; on what does it depend that these cells not merely remain aggregated together, but for the most part unite only in the form proper to the species? Is it that the attainment of one common result by a number of cells, each of which contributes to that result, depends on the mutual reaction of all the component cells, just as the different individuals in a state combine to obtain an object common to all, or as all the bees of a swarm contribute to its general economy? or are there certain dominant cells or monads to which the rest are subordinate, so long as they form part of the entire organism, as seems to be the case in the Hydra, portions of which when detached are capable of individual life, although while they form part of the entire polype they are subordinate to its form and will? But how is it that certain component cells of organised bodies, though similar to other cells and to the original germ-cell, nevertheless produce only cells of the same kind as themselves, and are totally incapable of acting as the germs of entire organisms? Why, for example, do the cells of the horny tissues cause the formation of new cells of the same kind in the nutrient matter in contact with them, and the cells of cartilage produce new cells within their cavity, and yet never become embryos or buds? and why do certain parts of the body of the Hydra, as the arms, when cut off, fail to grow into new polypes? The explanation of this latter difficulty may be that these cells, though endowed with the force which should reproduce the entire organism, yet in consequence of the special metamorphosis of their substance into horny or other matter have suffered such an impairment of their vital activity, that they not only fail to reproduce a new individual of the species when separated from the organism, but even while forming part of it lose the vital power of the germ, and fall off as particles of dead matter. These are questions and suppositions which naturally present themselves to our mind in the consideration of the foregoing facts, but they must not be regarded as necessary conclusions.

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* Schwann, op. cit. p. 227.

In this first theory, however, too great importance seems to be ascribed to the cells. The difficulties met with in applying it to the higher animals are so great, that its universality becomes highly improbable, though its correctness in the case of the lower organic beings is incontestable.

II. The second view which may be adopted is, that the power of reproducing the entire organism is not possessed by all the cells formed during the process of growth, and by the elementary parts of the tissues produced by their transformation; but, on the contrary, that this power at first resides in only one or a few cells which constitute the germ, and that, although it does undergo an increase during the process of growth, yet there arise at the same time many other cells, such as the cells of the horny, cartilaginous, and muscular tissues, which are endowed with the power of determining only the formation of new cells of their own kind. All the various cells of the organism, thus partial in their endowments and differing even chemically from each other, constitute together in the developed state what existed only in an undeveloped condition, or "potentially," in the germ-cell, or in the reproductive cells of the bud or gemma. Growth, therefore, partly consists in the conversion of the "potential" or undeveloped organism of a single cell, into a developed organism with many cells, specially endowed and distinguished both by structure and chemical qualities. Since, however, these cells, endowed with special subordinate functions, in their turn give rise to the formation, each after its kind, of new cells in the matter of the growing organism, and thus multiply themselves, the fully developed organism contains a multiple of its simplest elements. The body of the adult contains a multiple of the cartilage cells of the embryo, a multiple of its muscular fibres, &c.

The fully formed organism must not, however, be regarded as merely a fully developed individual; it is much more than this. It has still the essential force of the "potential" or undeveloped organism,—the power of multiplication by buds and generation; and this power is not the mere result of the mutual reaction of the special elementary particles of the developed organism, but is a force which still pervades the whole organism. This may be readily proved; for, independently of the fact that the head of a Hydra separated from its body will reproduce the body, we know that a man or a woman who has lost both legs still retains the power necessary for the generation of a perfect offspring, and would doubtless preserve that power if deprived of many other parts. Moreover, the mode of generation by the division, whether artificial or spontaneous, of a fully developed organism, shows us that there is a grade in the scale of organisation where the power of maintaining individual life and the structure of the species does not depend on the mutual reaction of all the various component particles or cells, but persists even when the sum of those particles is subdivided.

Further, it must be remarked, that from the earliest period of the growth of all organic beings, not merely the cells which constitute them as a developed organism are formed and multiplied, but cells or aggregates of cells are also produced, which represent " potential " individual organisms, or which, in other words, possess the power of themselves generating all the other cells which have special structures and functions in a developed organised body. During the growth of all organic beings, therefore, a double multiplication takes place,—namely, first, a multiplication of the particles constituting the existing form ; and secondly, a multiplication of this form (that of the species) in an undeveloped state,—that is, in the state either of the germinating bud or spore, or of the germ, which requires fecundation before it can undergo development. The substance capable of development without impregnation, in its simplest condition a single cell, may in some cases be formed at all or most parts of an organic body ; thus buds may be produced at almost any part of a Hydra or a plant. In other cases, the germinal substance is formed in a special organ,—namely, in the ovary, in the form of the germinal vesicles of the ova, just as the semen is formed in the testes. We have already observed, at an early part of this section, that all growth consists in the formation of a virtual " multiplum." We now perceive that this multiplication takes place in two ways,—namely, in the multiplication of the cells constituting as it were the mechanism of the individual organism, and in the formation of potential undeveloped multipla of this organism, in the form of primary or germ-cells. Both these modes of multiplication are in progress from the earliest period of development ; for, during the growth of the young sprout of a plant the germs of new buds are generated in it, and the ovaries of the child contain the germs for a new generation.

SECTION II.

Of Sexual Generation.

CHAPTER I.

OF THE SEXES.

In sexual generation the germs, though endowed with the power of propagating the distinctive properties of the genus and species, and even of the individual, are incapable of undergoing their destined organisation until they are acted on by another substance, allied to them, though distinct in its nature from them,—namely, the semen. The semen itself also propagates the peculiarities of the genus, species, and individual, but only by means of its influence upon the ovum, which is the immediate seat of all the changes attendant upon the production of a new individual.

The semen and ova are sometimes generated in different individuals, in which case fecundation is effected by the concurrence of the two sexes, or by the contact of the semen of the one sex with the isolated ova of the other, brought together, artificially, out of the body. Sometimes both semen and ova are formed in different organs of the same individual, which is the case in all hermaphrodite plants and animals. Dualism of the sex, therefore, does not necessarily involve dualism of the individuals ; on the contrary, sexual generation, as well as multiplication by buds and division, may be effected in a single individual.

Animals having only the female sex were formerly supposed to exist; and, indeed, all the lower animals, for example, the polypes, Acalephæ, and Echinodermata, were referred to that category ; ova being perceived in all the individuals of these orders of animals ; while the male organs, which are recognised less easily by the presence of spermatic animalcules, were not discovered. Since, however, double sexual organs are now known to exist in the Echinodermata, and since male organs have been demonstrated in the polypes, Medusæ, Radiata, and Infusoria,* the notion that any animals are of the female sex alone is quite inadmissible. Besides, an ovum, capable of undergoing development without impregnation by male semen, would not be an ovum but a deciduous bud or gemmule ; and an animal producing such germs could not be regarded as of the female sex. There are many animals which form buds, but these buds are not deciduous ; they undergo development on the parent stock. Some animals, as Cœnurus and Echinococcus, propagate by buds alone ; others, on the contrary, as the polypes, both by buds and ova. In the Hydra, the ova as well as the buds appear on the surface of the cylindrical body in consequence of the ovaries having that situation ; but the ova are distinguished from the buds by their hard horny shell.

In plants the male and female organs of generation are sometimes united in the same flowers ; sometimes developed in different flowers on the same stem (monœcious plants) ; and sometimes, lastly, wholly separated, different individuals of the species bearing either only male or only female organs (diœcious plants). The last mentioned arrangement of the sexes is the most rare in plants, while in animals it is very frequent, and in Insecta, Arachnida, Crustacea, and Vertebrata is universal. In plants of which the sexes are separate, it often happens that amongst the flowers of the prevailing sex a few of the other sex will show themselves, as is exemplified in Mercurialis annua, Spinacia oleracea, &c. In hermaphrodite animals fecundation is effected either by the concurrence of two or more individuals, or by each individual independently.

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* [The parts supposed by Ehrenbergh to be the sexual organs of the Infusoria are shown in figs. 146, and 147, page 1434.]

a. In the former case two individuals either fecundate each other simultaneously, the male organ of each impregnating the female organ of the other, which is the mode of impregnation in many Mollusca and worms (Annelida and Entozoa); or only one individual is impregnated in each act of copulation, the sexual organs being so placed that mutual impregnation is impossible; a condition, which Henley has observed to exist in the genus Helluo. In this animal fecundation is effected by the concurrence of two individuals; but while one introduces its penis into the other it does not itself receive the penis of the latter. In such cases, however, reciprocal impregnation is sometimes effected by the union of several individuals in a series, so that *a* is impregnated by *b*, *b* by *c*, *c* by *d*, and *d* by *e*. This mode of impregnation occurs in the Lymnæi, which are found, swimming in the water, thus united in a series. The last link of such a series of course is not fecundated, while the first does not fecundate.

b. In those hermaphrodite animals where fecundation takes place in each independently, it is generally effected by the semen finding its way to the ova within the body of the animal, as in the Radiata, according to Ehrenberg, and in the Distomata, according to Siebold. But in some cases the two kinds of sexual organs are repeated several or many times in the articulated body of the animal, and then two parts of the same animal may be bent towards each other and act respectively as male and female. It is not rare to find two tapeworms united and impregnating each other reciprocally. Once, however, a tapeworm has been observed impregnating itself; this observation was made in 1824 by a young naturalist, Fred. Schultze, whose early death was a loss to science. I was present when the fact was shown by Schultze to Rudolphi.*

The Articulata and Vertebrata present no instance of normal hermaphrodism. But in the other divisions of the animal kingdom nature has been so inconstant in respect of the sexes, that hermaphrodite orders, and orders with separate sexes, occur in the same class, and even families of both kinds in the same order.

The Infusoria, Radiata, Echinodermata, and Annelida appear, from the results of anatomical investigations, to be generally hermaphrodite.†

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* See Rudolphi, in Abhandl. der Acad. der Wissensch. zu Berlin, aus der Jahre 1825.

† [The existence of separate sexes in the Echinodermata has been observed by Va-

In many of the Infusoria Ehrenberg has discovered the male and female organs. The Polypi are likewise for the most part hermaphrodite. Amongst the Campanulariæ, however, they are, according to the observations of Ehrenberg and Lowen, distinct male and female individuals. Many polypes of the stock were observed by them to have all the organisation necessary for individual life, whilst in others the arms and internal organs essential to individual life, were atrophied, and these appeared to be converted into ovaries. These metamorphosed polypes had, indeed, been previously described as ovaries by Cavolini and others.* Nordmann has published similar observations respecting his Tendra zostericola, in which the male and female cells are situated close to each other. The testes of the male polype consist of eight vermiform organs placed near the tentacles. The ova of the female cells are fecundated by the spermatic animalcules of the male polypes.† In other polypi, as the Actiniæ, both ovaries and testes are known. R. Wagner‡ has discovered seminal animalcules in convoluted tubes of the Actiniæ. Similar tubes have been seen by Edwards§ in compound Polypifera; but it is not known whether they contain seminal animalcules.‖ Amongst the Acalephæ the Medusæ, at least, appear from the recent researches of Siebold to possess separate sexes. The males of the Medusa aurita are smaller than the females,—have not the small sacs in the tentacles, and never contain ova. In the testes of the male Medusa, Siebold has detected spermatozoa.¶

The class Entozoa includes genera devoid of sexes, hermaphrodites and genera with the sexes in distinct individuals. The Cœnurus and Echinococcus among the Tænioidea cystica (the Cystica of Rudolphi) seem to propagate wholly by the development of buds. The Tænioidea cestoidea (the Cestoidea of Rudolphi) are hermaphrodite, and afford instances both of self-impregnation and of reciprocal impregnation. In the animals of this order the generative organs and their external openings are repeated in all the fully developed segments,

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lentin (in the Holothuria and Spatangus), Wagner (also in the Holothuria), Rathke (in the Asterias and Ophiura), and by Peters (in the Echinus). See Valentin in Froriep's Notizen, bd. xii. No. 7, and Repertor, 1840, p. 301. Rathke, Froriep's Not. b. xxi. No. 269, and No. 331. Peters, Müller's Archiv. 1840, p. 144.]

* See Lowen, in Wiegmann's Archiv. iii. p. 249.

† Ann. des Sc. Nat. xi. p. 185.

‡ Wiegmann's Archiv. i. No. 5, 213.

§ Ann. des Sc. Nat. 1835, December.

‖ [Edwards has since detected Spermatozoa in these tribes of the Polypifera (Ann. des Sc. Nat. 1840). Van Beneden describes distinct males and females in Alcyonella (Ibid.), and Erdl has observed that part of Veretillum is male and part female (Froriep's Notiz. 1840, No. 249). See also Wagner's observations on the separate sexes of the polype, Veretillum, Froriep's Notiz. xii. No. 7. Dr. A. Farre observed a number of animalcules, like Cercariæ, in the visceral cavity of Sertulariæ. Phil. Trans. 1837, Pt. ii.]

¶ See Müller's Archiv. 1837, p. 438.

and the fecundated ovaries are sometimes excluded from the segments containing them, and sometimes separated together with those segments. The ova, therefore, do not escape by the same orifices through the medium of which they were fecundated. The orifices of the sexual organs are, according to Mehlis,* very differently placed in the different genera of the Cestoidea. Thus, in the Bothriocephali, the two orifices are situated one in front of the other in the middle of the abdominal surface of each segment. In the genus Tænia, they are found at the bottom of a cup-shaped depression at the margin of the segments: and in the genus Triænophorus, the orifice of the male organ is at the margin, that of the female organ in the middle of the segment. The fluke-worms, Trematoda, are almost without exception hermaphrodite. Some of them have been regarded as devoid of sex; but probably, without reason, since the phenomena of the generation of such worms would rather accord with a diœcious disposition of sexes. Animals of this doubtful nature are the Cercariæ generated in the body of snails, in tubes which are free, and generally, though not always, present independent movements, but which have been called ovistocks or germ-stocks. These moving tubes, the yellow worms of Bojanus, to which great attention has been directed by the observations of Nitzsch, Bojanus, Von Baer,† and Von Siebold,‡ are evidently organised, and in some cases can be seen to have a cœcal digestive cavity. They vary in form according to the species of Cercariæ which they contain. The Cercariæ lie in different stages of development between the outer tube and the intestinal cœcum, and move freely. After their escape from the tubes, they throw off their tail and envelope themselves in a new covering, so as to assume the state of a chrysalis; and what further change they undergo is not known. The observation of Siebold, that the parent tubes sometimes contain, together with the Cercariæ, young tubes of the same form as themselves, suggests the suspicion that both the tubes and the Cercariæ belong to the same species of animal; that the tubes are the fructiferous individuals, and the Cercariæ either males or individuals of no sex. We have instances in other animals,—for example in Lernææ,—of the female departing very considerably from the form of the species; and we have already mentioned that among the Polypi entire individuals are sometimes converted into ovistocks. The ramified and fixed germinal tubes containing Distomata, which Carus § has described, are, however, quite enigmatical; and it is equally difficult to explain the fact observed by Von Siebold, || that the embryos of Monostomum

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* Isis, 1831, p. 69.

† Nov. Act. Nat. Cur. t. xiii. pt. ii.

‡ Burdach's Physiologie, bd. ii. 2te Auflage.

§ Nov. Act. Nat. Cur. t. xvii. pt. i.

|| Wiegmann's Archiv. i. p. 45.

mutabile contain a parasite of the form of the yellow worms of Bojanus, which entirely fills their cavity. Is this the result of metamorphosis occurring during embryonic life?

Other entozoa, namely, all the Nematoidea of Rudolphi, as the Ascaris, Strongylus, Oxyuris, Spiroptera, Trichocephalus, and Filaria, have the sexes on distinct individuals.

Some worms also which do not belong to the class Entozoa, as, for example, the genus Gordeus, have the sexes distinct, and in that respect resemble the nematoid Entozoa. The Planariæ, on the contrary, are hermaphrodite, as are likewise all the Annelida.

Of the Mollusca, one entire order, the Cephalopoda, have the sexes distinct, while the Gasteropoda and Acephala have both hermaphrodite genera, and genera with distinct male and female individuals. The majority of the genera of Gasteropoda are hermaphrodite; the Pectinibranchiata, however, as the Tritonium, Murex, Paludina, &c. have the sexes distinct.*

The existence of the two sexes in the order Conchifera was known to Leeuwenhoek, who recognised the ova and spermatozoa in distinct individuals; and this discovery, which was long neglected, has been recently confirmed in the most conclusive manner by Von Siebold. The ovaries or testes lie at each side of the foot, where this organ exists, and resemble each other very closely in external characters; but are distinguished by microscopic examination; the ovaries of the female being found to contain merely ova with their essential parts, the germinal vesicle and germinal spot, and the testes of the male only spermatic animalcules. According to Siebold's researches,† the genera Anodonta, Unio, Mytilus, Tichogonia, Tellina, Cardium, and Mya, and, according to my own observation, Pholades also, have the sexes thus distinct. Some conchifera, however, have the sexes united; for Wagner found both ova and spermatozoa in all the individuals of the genus Cyclas.‡

Insecta, Arachnida, Crustacea, and all Vertebrata have the sexes distinct; and the erroneous assertion that hermaphrodite genera, or genera having only the female sex, exist amongst them, has arisen from the superficial observation of the general similarity of form which the sexual organs sometimes present, for example, in many fishes; or from the comparitive rarity of the individuals of one sex, as, for example, of the males in the genus Apus.

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* The Patella and Chiton also have been observed by R. Wagner (Froriep's Not. xii. p. 7) to have distinct sexes. See also Edwards and Peters (L'Institut. 1840, No. 334), on the existence of distinct sexes in the genera Carinaria and Firola.

† Müller's Archiv. 1837, p. 381.

‡ See also Edwards on the hermaphrodism of the Pecten. L'Institut. 1840, p. 336. Krohn (Froriep's Notiz. No. 356, 1842) says that the bivalve Clavagella is hermaphrodite. And Neuroylen states that the Bojanus's lung of the bivalves (Unio and Anodonta) is really a testis, and consequently that all these animals are hermaphrodite.

In these classes, when the sexes are distinct, the individuals may be either male, female, or of no sex, though, more correctly speaking, the individuals of the latter kind are unfruitful females, or at least females arrested in their development, since they contain imperfect ovaries. Individuals of this third kind occur in several genera of insects, as Bombus, Apis, and Formica. Those of the bee kind are called working-bees. The unfruitful ants are destitute of wings, and are directed by their instinct to protect and nourish the larvæ. The imperfect females or working-bees of the genus Bombus are not indeed incapable of pairing; at least some of those which come out of the larva state in the spring do, according to Huber, pair with the males of the same generation; but they produce only males. These latter males alone are destined to fecundate the proper or perfect females, the brood of which forms a new colony. Amongst the true bees, Apis mellifica, the working bees are smaller than the perfect females, though they resemble them in many respects. The working bees are barren; but they are rendered fruitful if, while in the larva state, and very soon after their escape from the egg, they receive a particular kind of food, namely, that destined for the nourishment of the queen-bee; and if they are at the same time placed in a larger cell they acquire all the properties of the queen-bee. If, however, after having received the food proper for the queen-bee, they are placed in a small cell, they produce only males, and are distinguished from the perfect female by their smaller size. The working-bees, therefore, are females, the ovaries of which, in consequence of the nature of their food during the larva state, have remained undeveloped, and which, at the same time that they have suffered this imperfect evolution, have received special instincts. A swarm of bees consists of about fifteen or twenty thousand working-bees, six or eight hundred males, and a single perfect female.*

Instances of the arrest of development of the male or female sex without any approach to mixture of the characters of the two sexes, or to a true confusion of the sexes, occur also as an abnormal condition in the higher animals and the human species; and these cases must be distinguished from those of abnormal mixture of the sexual characteristics or hermaphroditism. The subjects of hypospadia, in whom testes are present, and still more the eunuch, are imperfect males.

The individuals of the two sexes in each species of animal are generally distinguished by peculiarities of form, and often also by peculiar colours, or even by difference of size. Sometimes the female is larger, occasionally even to an extraordinary degree larger than the male, as is the case for example in the genus Lernæa, where the tiny male remains through its entire existence fixed over the orifice of the sexual organs of the female.* In other instances, as in many birds, the male excels the female both in size and strength, and in the beauty of his markings.† The most important differences, however, between the two sexes are those evinced in their instincts, which are more constant than the differences of form. The female is entrusted with the protection of the offspring, and for this purpose dreamlike incentives to action, or instincts, arise in her sensorium. As soon as the egg is laid and seen, the female bird feels an instinctive attachment to it, and never leaves it except for short periods. The females of Mammalia have the same maternal instinct after the birth of the offspring. The young animal seems to form part of its mother, who protects and defends it in all dangers. The entire or principal care of the young belongs for the most part to the female; and the case of the male Alytes obstetricians, which bears the ova upon its feet, is a rare exception.

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* See Latreille in Cuvier's Règne Animal, t. v. p. 361. On the ovaries of the working-bees, consult Ratzeburg, Nov. Act. Nat. Cur. t. xvi. pt. ii.

The male of the human species is of larger proportions, stronger build, and more marked outline than the female; has respiratory and vocal organs of larger dimensions; is less easily affected by external impressions; and is in every respect not only physically but also morally of greater strength. He yields less easily to pleasant and unpleasant or painful feelings, is more energetic and constant in his efforts and desires, and more courageous; but he is also more selfish, and more ambitious of honour and fame. He excels the woman in capacity for all intellectual labours and in fruitfulness of mind; and is more cautious, systematic, and reserved in his intercourse with his fellow-men, more difficult to turn, and more haughty; but at the same time more upright and magnanimous. The field of his activity lies in the intercourse and contest of human faculties,—in the relations of society.

The woman, more delicately formed, is weaker both in body and in the faculties of the mind than the man; she is more excitable and sensitive, more timid and pliant, more superstitious, more vain, more excited by feelings of pleasure and disgust, and less so by desires. She is gifted with finer feelings of propriety and adaptation, and with a lively imagination; but is without the creative power and the clearness of intellect of the man; while, on the other hand, the reproductive power of her body is greater. Friendship towards her own sex is rare in woman, but her love for her husband and children is proportionately strong; so that her whole mind may be occupied by those feelings. Moreover, woman is distinguished by her modesty, meekness, patience, and amiability; by her readiness to sacrifice her own good and herself for the sake of others; by her tenderness, sympathising disposition, and piety. The field of her activity is her home and family.*

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* See Nordmann, Microgr. Beiträge.

† For an account of the varieties presented by the animal kingdom in this respect, consult Rudolphi's Beiträge zur Anthropologie. A complete history of the phenomena of the sexes will be found in Burdach's Physiologie, bd. i.

We have already seen how the male and female reproductive substances, the semen and ovum, differ from the bud or gemma. Like the bud, they have the faculty of reproducing the form of the parent organism; the semen, namely, gives the individual peculiarities of the male, and the ovum those of the female. Unlike the germ of buds or gemmæ, however, both the ovum and the semen are imperfect, inasmuch as neither can manifest the reproductive power until it is united with the other. In hermaphrodite animals the two imperfect substances which are thus complementary of each other are formed in the same organism; in animals with distinct sexes they are formed in different individuals, and these individuals of different sexes, though perfect in all the characteristics of the species, yet are in respect of the reproductive power both imperfect, and therefore seek each other, as it were for the purpose of supplying the deficiency. This fact is represented figuratively in the "Banquet" of Plato by the fable of the two halves of a human body.

CHAPTER II.

OF THE SEXUAL ORGANS.

THE sexual organs consist, in both sexes, of a formative organ, the testis or the ovary, and of an efferent organ, the oviduct, or the vas deferens. In the female efferent organ, the ovum in its passage from the ovary generally becomes invested by some new secretions, which are either destined to serve as nutriment, or to form a shell. In many animals one part of the oviduct also forms the receptacle for the ovum during its development, and is called the uterus. A uterus in this sense exists in the viviparous genera of Fishes, Amphibia, and Mammalia, as well as in Man. The secretion of the testes also in its course to the exterior of the body becomes, in many cases, mixed with other secretions, which are poured out by accessory secreting organs connected with the male efferent organ. In those animals in which the two sexes are distinct, but in which impregnation is effected internally, there are superadded at the orifice of the efferent apparatus the organs of sexual connection. The essential sexual organs, however, which are universally present, are the formative organ and the efferent apparatus. The sexual organs of both sexes present two perfectly distinct types, which are characterised by the relation which the formative and efferent organs bear to each other. In one type the efferent organ has the place of a true efferent duct, its walls being continuous with those of the cavities of the formative organ; in the other, the two essential parts of the sexual organs are wholly unconnected, and the ovum, or semen, first makes its way through the parietes of the formative organ into the abdominal cavity, and escapes thence by a special canal. The product of the formative organ may in this case either fall free into the abdominal cavity before making its way out by the efferent canal, or it may be at once received from the ovary or testis into the open end of the tube which is not far distant.

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* Compare Rudolphi Physiologie, bd. i. p. 259.

The male sexual organs of all Invertebrata, and of by far the greater number of the Vertebrata, are formed after the first type,—that in which the efferent part is continuous with the formative part of the apparatus. Such is their form in Man, Mammalia, Birds, Reptiles, Amphibia, and most Fishes. The female sexual organs are less frequently formed after this type. They are, it is true, formed in this manner in most Invertebrata; but the contrary is the case in Vertebrata, with the exception of the osseous fishes, in the greater number of which the ova are formed in the walls of a hollow tube,—the prolongation of the oviduct; so that the ova escape at once into the interior of the efferent duct, and never pass at all into the abdominal cavity.

It is seldom that the male sexual organs are formed in accordance with the second type, in which the efferent duct opens directly out of the abdominal cavity, and has no communication with the testis. They have never this form in Invertebrata, and among the Vertebrata only in some few fishes,—namely, the Cyclostomata, (the Petromyzon, Ammocœtes, and Myxinoidæ,) and in eels. Rathke has discovered the existence of the structure of the male organs just described in nearly all those fishes. The testes of the male Petromyzon is a cellular organ attached to the vertebral column. In the month of May the abdominal cavity is full of fluid semen, which, under pressure, escapes in a full stream from a papilla situated close to the anus. The canal through which the secretion here escapes from the abdominal cavity is extremely short, and is not elongated into a tube within the abdomen. The escape of the semen is effected in exactly the same manner in the myxinoid fishes and in eels.*

The female sexual organs of Invertebrata are very rarely formed after the second type; the only instances of their having that structure, with which I am acquainted, occur in the Echinorhynchus, where, according to Von Siebold, a separate efferent tube, or oviduct, opens by a funnel-shaped extremity into the abdominal cavity, while the ova escape into the abdominal cavity before they are received into this tube to be conveyed by it out of the body; and in the Sepia, in which, also, Krohn† has observed the ovary and oviduct to be separate. In vetebrate animals, on the contrary, this type is the prevailing one: the only exception to it being met with in osseous fishes. The simplest form of the female efferent organ, when it is distinct from the ovary, is found in the Cyclostomata, in eels, the Cobitis tænia, and in the Salmonidæ; in which fishes it is a simple opening leading from the abdominal cavity to the exterior. In the female Petromyzon, the abdominal cavity is in the month of May full of ova, which flow out of the opening just referred to, when the belly of the fish is compressed. In the sturgeon,—Acipenser sturio,—similar openings exist, and the ova may escape from the abdomen through them, or through funnel-shaped tubes which communicate with the ureters in both sexes. In Acipenser huso, and others of the sturgeon family, the external abdominal openings do not exist, and the funnel-shaped tubes communicating with the ureters are the only means of escape for the ova. In the sharks and rays, reptiles, Amphibia, birds, and Mammalia, the short efferent canal of the Cyclostomata is extended into a long tube,—the oviduct. The end of this tube, which opens into the abdominal cavity, sometimes lies close to the ovary, as in man, Mammalia, and birds; and in the seals, otters, martens, and ferrets its dilated extremity appears, from the observations of Albers, E. H. Weber, and Treviranus,* to envelope the ovary in the manner of a capsule; whilst in other cases, the ovary and the infundibulum of the oviduct are at a considerable distance from each other, as in the sharks and rays and Amphibia. In the shark family, the two oviducts meeting above the liver form there a common infundibulum, while the ovaries lie on the outer side of the liver, or beneath it. In the rays and Amphibia the two oviducts remain distinct; but even in the latter class they extend to the most anterior part of the abdominal cavity, far beyond the ovaries.

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* See Rathke's Beiträge zur Geschichte der Thierwelt, p. ii. and Müller's Archiv. 1836, p. 178.

† Müller's Archiv. 1839, p. 353.

Many animals have but one ovary, and many, indeed, only one oviduct. In the myxinoid fishes the ovary is single, and is situated to the right side of the mesentery, suspended by a special fold of peritonæum. Scyllium carcharias, and Mustelus, among the shark family, have a single ovary, which in them lies in the middle line. In many osseous fishes, also, Rathke found both the ovary and the testis single. In most birds, the Raptores excepted, only the left ovary and oviduct are developed, the right existing in the embryo, but becoming atrophied.† The reverse of this condition is presented to us in the multiple ovaries of some animals. The Tænioidea cestoidea, which do not propagate by the formation of gemmæ, like the cystoid worms, but are distinguished by their jointed structure, and by the repetition of the male and female sexual organs in each of the fully-formed segments, afford a remarkable example of the multiplication of the sexual organs without multiplication of the indivi-

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* See Tiedemann's Zeitschrift, i. p. 180.

† See Wagner's account of the Predacious Birds, with double ovary and oviduct, in the Abhandl. der K. Baiersch. Acad. ii. 1837.

dual. The gemmiparous cystoid worms are compounds of many individuals united on a single stock. In many cestoid worms, also, separate segments fully formed become detached with thousands of ova contained within them. A similar example of equally great multiplication of the ovaries is presented to us in the Comatulæ and Crinoideæ among the Radiata, in which each pinnula of the arms contains an ovary, so that one Comatula has a thousand or more ovaries.* Here, again, only the generative organs are multiplied, the animal remains a simple individual; and we are reminded of the multiplication of the sexual organs in plants.

The oviducts either open separately into a cloaca, as in fishes, reptiles, and Amphibia; or previously coalesce to form a single median tube. The uterus either is single, as in apes, or has two cornua, or is perfectly double. The true double uterus exists in the sharks and rays, and in several Mammalia,—namely, in the greater number of the Rodentia, the Ornithorhynchus, &c. In Ruminantia, Pachydermata, Solidungula, Carnivora, and Cetacea, the uterus has a single body and external orifice, but has two horns. The uterus of the Marsupiata is peculiar in its structure. The middle part, or body of the organ, terminates inferiorly in a *cul de sac*, without having any communication with the vagina, but gives off two cornua superiorly, and two other cornua laterally, which pass downwards, and open into the vagina.

In many cases where impregnation is effected within the female sexual apparatus, special organs of intromission are provided. They do not, however, seem absolutely necessary for that purpose; for there are many animals in which impregnation is internal, and in which it is effected merely by the cloaca of the male, or the papilla of the seminal ducts being applied to the cloaca of the female, as for example in the viviparous Amphibia and many birds.

The males of fishes, and all the Amphibia, and also of the singing and predacious birds, are destitute of penis. In many other birds, on the contrary, in reptiles and in Mammalia, this organ is present. The penis, the organ through the medium of which the pleasure of the act of coition is excited in the male, and by which the semen is conveyed into the interior of the female sexual organs, is not formed after the same type in all classes of animals. There are two perfectly distinct forms of the penis, which are not modifications of the same type, but are sometimes associated together.

1. The first form is that presented by the organ of intromission in the Crocodilida and Chelonia, in the ostrich (Struthio camelus), and in Mammalia. Here the penis consists either of two solid fibrous bodies, as in Chelonia and Crocodilida, or of two bodies, fibrous only on the surface, and internally cellular, and capable of erection, as in Mammalia. These bodies are united in the middle line, and are fixed at the abdo-

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* See J. Müller, in Müller's Archiv. 1837. Jahresb. p. xcvii.

minal aspect of the external sexual region. At their inferior or posterior surface there is in crocodiles, tortoises, and turtles, the ostrich, and the young fœtus of mammalia, a groove invested with mucous membrane and cavernous tissue. This groove, which is the cavity of the corpus cavernosum urethræ, not yet closed, remains permanently in that condition in the Crocodilida, Chelonia, and the ostrich, but in Mammalia and man becomes closed, so as to form a tube of which the glans penis is the continuation. In many monkeys, bats, and rodent and carnivorous animals, the anterior portion of the penis and glans (which is often very much elongated) contains a portion of bone destined to support the canal. In the wading birds the rudiment of a penis often exists in the form of a lip or tongue, with a groove at its posterior surface, which looks towards the cloaca. The ostrich has besides the two fibrous bodies of the penis a third elastic body, which retracts the penis when it is not in the state of erection, causing it to become spirally bent. This third body is cavernous or cellular internally, and hence is enabled also to extend the penis.

Of the three cavernous erectile bodies which exist in Mammalia, one only is found in the Crocodilida, Chelonia, and ostrich,—namely, that of the urethra, which is cleft.

2. The second form of the penis occurs distinctly only in serpents and lizards. The organ of intromission here lies, not at the abdominal, but at the dorsal or caudal boundary of the external sexual region. It consists of a hollow cæcal tube, the walls of which contain erectile tissue. The open end of this tube is directed forwards, towards the cloaca, and on its inner surface there is a groove. In serpents and lizards there are two such organs. During the act of copulation they are everted, as we may evert the finger of a glove, and then the groove comes to be placed on their exterior, and serves to conduct the semen from the cloaca. In the viper kind, Crotalus and Python, each of the tubular organs we have described is bifurcate at its cæcal extremity, so that when everted, the penis appears forked. In serpents and lizards the penis is retracted and inverted again after erection by muscles which are attached to the cæcal end of the tube.

3. In ducks, geese, and the rhea, cassowary, and emeu, the first and second forms of the penis occur in combination with each other. Here there is a solid portion attached to the anterior or abdominal wall of the cloaca, formed of a fibrous structure, and having a groove on one surface, and another tubular portion of the same structure as the penis of serpents and lizards, and like it capable of eversion. The latter part is here, however, not double, and, except during the venereal orgasm, lies convoluted, like a piece of intestine, near the cloaca. The open end of this tube is situated at the extremity of the solid portion of the penis, and in the act of coition it becomes everted and protruded, so as to give

the penis double the length which the solid portion alone possesses. The groove on the interior of the tube becomes placed on its exterior when it is erected, and then forms a continuation of the groove of the fibrous portion of the penis. After the act of coition is completed, the tubular part of the penis is retracted, and again inverted by an elastic band.*

The females of the duck and goose kind, and of the rhea, cassowary, and emeu, have a clitoris formed on the same type as the male organ, though of much smaller dimensions.

The clitoris of Mammalia has the same structure as the penis of the male in the embryo condition: both are formed on the same principle. The clitoris of the female embryo (which is then proportionally large), and the penis of the male, at first resemble each other exactly in external form. In both the corpus spongiosum s. cavernosum urethræ is cleft, so as to form on open canal. Both, also, have musculi ischio-cavernosi (erectores penis s. clitoridis) and constrictores pudendi. But when the perinæum closes in the male, the latter muscles form the acceleratores urinæ. The clitoris, on the other hand, becomes shorter, and the lips of its groove are converted into the nymphæ. As long as the perinæum remains open, the place of labia externa is supplied in the male fœtus by the folds which afterwards form the scrotum, but which are as yet empty, the testes being in the abdominal cavity. In many of the Mammalia, as the Cetacea, Ornithorhynchus, elephant, and Hyrax, the testes never leave the abdomen; but in most mammals, and in the human subject, they descend before the termination of fœtal life, lodged in a fold of peritonæum into the scrotum; and subsequently the diverticulum of the peritonæum, which descends with them, becomes cut off from the abdominal cavity. In several animals, again, as the rat family, the hamster, and others, the communication between the cavity of the abdomen and that of the scrotum remains open, and the testes may, by the action of muscles, be brought to be at one time within the abdominal cavity, and at another time external to it.

In the genus Stenops, among the monkeys, the urethra traverses the clitoris, although the vagina has its usual position, more posteriorly.

CHAPTER III.

OF THE UNIMPREGNATED OVUM.

Our knowledge concerning the unimpregnated ovum has been brought to its present state by the labours of modern anatomists, particularly by the exertions of Purkinje, Von Baer, R. Wagner, Coste, and Valentin. So successful has been their study of this subject, that in it, as in all the most perfect parts of science, the numerous individual facts can now be referred to simple laws.*

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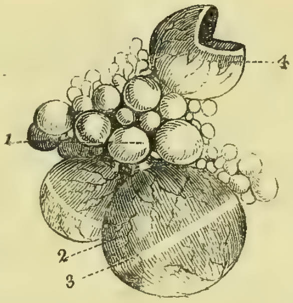
* See J. Müller, in the Abhandl. der Acad. der Wissensch. zu Berlin. 1836.

In many invertebrate animals the ova are developed in the interior of cæcal tubes, in which they are not surrounded on all sides by organised tissues, so as to be separated from each other; but in many other of the Invertebrata, and in all the Vertebrata, they are formed within the cells of the ovary. These cells are invested singly by numerous blood-vessels, and are united together by a fibrous substance of a greater or less degree of firmness, called the *stroma*. When the ova lie in insulated cavities of the ovary, the wall of these cavities, formed of the condensed stroma, is called the capsule or *theca*. The following essential parts may be distinguished in the ova of invertebrate animals, fishes, Amphibia, reptiles, and birds,—even in those of the smallest size.

1. The capsule of the ovum, *ovicapsule*, which is in some cases, as in many Invertebrata, insulated from the proper tissue of the ovary, and may even escape with the ovum; but which in other instances, as in the oviparous Vertebrata, coalesces with the theca of the ovary, forming there what is termed the *calyx* (see figs. 152^{4}, and 154^{1}). On the side directed from the ovary the calyx is often thin, but is thicker on the side next to the ovary, to which it is connected merely by a pedicle (figs. 152 and 154). The thin side of the calyx in the ovary of the bird often presents a white band, of an arched form, and distinguished from the rest of the calyx by the absence of blood-vessels (fig. 152^{3}). This band, the *stigma*, indicates the situation at which the dehiscence of the calyx will subsequently take place to allow

Fig. 152.†



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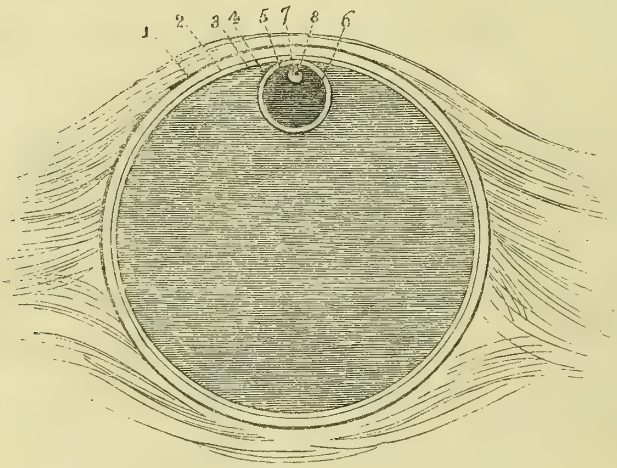
* The following are the most important works on this subject:—Purkinje, Symbolæ ad ovi avium historiam ante incubationem, Lips. 1830; and Encyclop. Wörterbuch der medic. Wissensch. Art. Ei. Von Baer, De ovi mammalium et hominis genesi, Lips. 1827. Coste, Recherches sur la génération des Mammifères, Paris, 1834. Bernhardt (et Valentin), Symbolæ ad ovi mammalium historiam ante imprægnationem, Vratislav, 1834. Valentin, Entwickelungs-geschichte, Berlin, 1835. R. Wagner, Müller's Archiv. 1835, p. 373; Prodromus historiæ generationis hominis atque mammalium, Lips. 1836; Abhandl. der K. Baiersch. Acad. 1837, p. 2; and Lehrbuch der Physiologie, Icones Physiologicæ, Leipz. 1839. Krause in Müller's Archiv. 1837, p. 26. Carus, ibid. 1837, p. 442. Jones, London Med. Gazette, 1838, p. 680. Schwann, Mikroskop. Untersuch. Barry, Philos. Transact. 1838 [and 1839]; and Edinburgh Philos. Journal, 1839. The best figures of the ova of Invertebrata given by the older writers are those of Poli, Goeze, Della Chiaje, and O. Fr. Müller. The ova of fishes had been best shown by Cavolini, Erzeugung der Fische und Krebse, tab. i. fig. 4; and Sonnini, Hist. Nat. des Poissons, t. ii. tab. iii. fig. 4. The structure of the ova is correctly indicated, though it was not understood by these writers.

† [Figure of the ovary of a common hen, after Carus. 1, imperfectly developed

the escape of the ovum. Schwann has observed a circumstance which is worthy of remark, as aiding in identifying the capsule of the ovum of different classes, — namely, that a stratum of epithelium cells exists on the inner surface of the ovicapsule in fishes, and also on the inner surface of the *Graafian vesicles* or capsules of the ova of Mammalia. Both Jones and Barry, with justice, regard the ovicapsules of oviparous animals as identical with the Graafian follicles of Mammalia (fig. 153$^{2\ 3}$).

Fig. 153.*



2. Within the ovicapsule lies the *yolk*, surrounded by the *vitelline membrane* (fig. 153$^{6\ 5}$, and 154$^{5\ 4}$). This membrane is at first in close contact with the capsule, but subsequently becomes separated from it in many animals by a tolerably large interval. The granules of the yolk are found by Schwann to be cells containing a finely granular matter and oil globules.

3. In the substance of the yolk is imbedded the *vesicle of Purkinje*, or vesicula germinativa (fig. 153^{7}). This vesicle is of greatest relative size in the smallest ova, and is in them surrounded closely by the yolk, nearly in the centre of which it lies. During the development of the ovum, the germinal vesicle increases in size much less rapidly than the yolk, and comes to be placed near to its surface. Ovula and germinal vesicles can frequently be detected in the ovaries of the fully developed embryo.

4. The germinal vesicle contains a transparent fluid, and in addition to this, the *germinal spot*, macula germinativa, or nucleus germinativus of R. Wagner (fig. 153^{8}). This germinal spot consists of one or more

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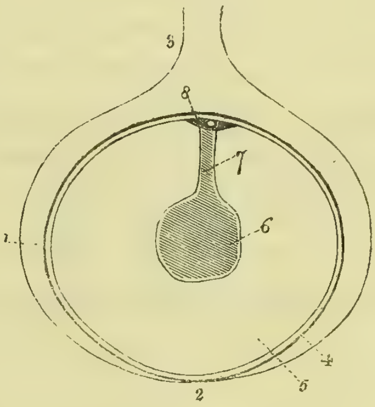
ova; 2, an ovum nearly fully developed in its calyx; 3, the stigma, or line of dehiscence; 4, a calyx from which the ovum has escaped.]

* [Diagram of an ovicapsule, or Graafian vesicle of a mammal, containing the ovum. 1, Stroma or tissue of the ovary; 2 and 3, external and internal tunics of the Graafian vesicle; 4, cavity of the vesicle; 5, thick tunic of the ovum or yolk sac; 6, the yolk; 7, the germinal vesicle; 8, the germinal spot.]

somewhat opaque corpuscules, and is possibly the analogue of the nucleus of formative cells. It is simple in the germinal vesicle of the human subject, of Mammalia, birds, reptiles, and many Invertebrata, and is recognisable even in the ova which are least advanced in development. In Amphibia, the osseous fishes, and several invertebrate animals, the germinal spot is multiple. As the ova advance in development granular matter is deposited on the inner surface of the germinal vesicle, and renders the germinal spot or spots indistinct, and sometimes even invisible. In some of the Invertebrata the germinal spot itself seemed to Wagner to have a special investing membrane.

In the larger and fully formed ova of the oviparous Vertebrata, the germinal vesicle is found lying at the surface of the yolk, imbedded in a disk-shaped layer of granular substance, the *germ-disk*, or discus proligerus of Baer (see fig. 154 ^{8}). The vesicle is prominent above the surface of this disk, which is continued from side to side beneath it. The middle of the yolk is occupied by a kind of cavity filled with a more transparent mass, and from this cavity a canal, filled with a similar substance, extends towards that point of the surface at which the germinal vesicle is situated (fig. 154). The substance filling this cavity and canal of the yolk is found by Schwann to consist of cells, distinguished from the ordinary cells of the yolk by their smaller diameter, and by their containing a nucleus. The part of the yolk in which this canal and the germinal vesicle, or the germinal disk are placed, is lighter than the other parts, and, consequently, in ova which have acquired the albumen and shell in their passage through the oviduct, the yolk always places itself so that the germ lies uppermost, whatever the position of the entire egg may be.

Fig. 154.*



It results from the observations of Purkinje and Baer, that the germinal vesicle disappears at the time when the ovum leaves the ovary, and before impregnation has taken place. Baer found no germinal vesicles in the ova of frogs which had reached the oviduct: the vesicle appears to dissolve away and to mingle its substance with the granular mass of the germinal disk. In the hen's egg the germinal disk measures about one line in diameter; it is seen immediately under the vitelline membrane in all eggs which have left, or are about to leave the ovary, whether they are impregnated or not; in it the first rudiments of the embryo are formed. Beneath the germinal disk in the hen's egg there is a granular mass called the *cumulus proligerus*, nucleus cicatriculæ, or nucleus of the germinal disk. This mass consists, according to Schwann, of cells similar to those of the transparent centre of the yolk, while the germinal disk itself is composed of cells filled with coarse granular matter.*

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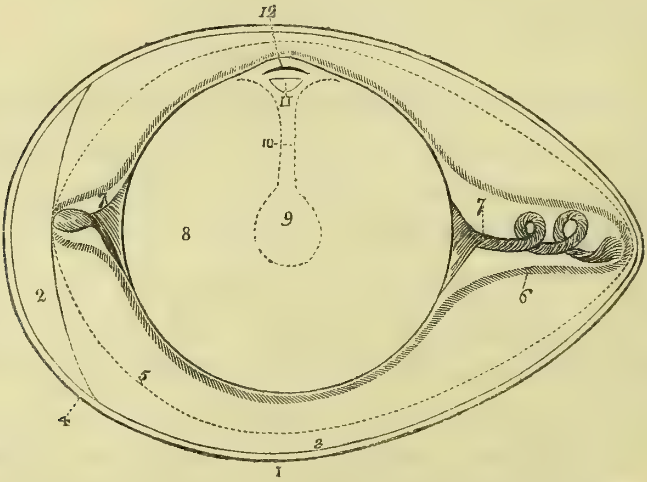
* [Diagram of a calyx from the ovary of a bird, containing a fully-developed ovum cut perpendicularly, after Von Baer. 1, The calyx; 2, situation of the stigma where the calyx is attenuated; 3, the pedicle of the calyx; 4, the yolk sac; 5, the yolk; 6, the yolk cavity; 7, the canal; 8, the germinal disk, or discus proligerus, with the germinal vesicle.]

The ova of oviparous Vertebrata, when they leave the ovary, consist merely of the yolk with the vitelline membrane, and the other parts contained within these. The albumen and shell are added in the oviduct.

The separation of the ova from the ovary may take place independently of impregnation: such is the case, for example, in frogs and in birds. The ova of frogs, indeed, always leave the ovary and are received into the oviduct long before their impregnation, which is not effected until they have wholly escaped from the body of the female. After the separation of an ovum its calyx remains; but it gradually wastes and becomes confounded with the mass of the ovary. In the oviduct of many oviparous animals the ovum receives an investment of albumen, which is secreted by the tube. In birds, the more dense internal layer of this albumen, which adheres to the yolk, is continued in the form of two spirally twisted bands towards the extremities of the egg; these are the chalazæ, which are produced by the revolving motion of the egg in its descent through the oviduct (see fig. 155). The shell

Fig. 155.†



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* [Dr. Martin Barry's account of the changes which the germinal vesicle undergoes at the time of impregnation, and of the other immediate consequences of the action of the semen on the ovum, differs in many important respects from that given in the text. It will be found in the 5th Chapter of the present Section.]

† [Diagram of a bird's egg after impregnation, supposed to be cut perpendicularly, after Von Baer's figure, as modified by Wagner. 1, Shell; 2, folliculus aeris; 3, membrana testæ, which divides into two layers at 4; 5, boundary of the more dense middle

also is due to the secreting action of the oviduct. The oviducts of sharks and rays are furnished with two large glands for the formation of the horny shell of their ova. The shell of the bird's egg consists of the membrane of the shell, and of the carbonate of lime deposited thereon. The lining membrane of the shell is itself composed of two laminæ, which separate from each other at the large end of the egg, in proportion as the fluids of the egg evaporate, and thus form the folliculus aeris (fig. 155 [2]), which is found in that situation in all eggs which are not perfectly fresh.*

The ova of Mammalia and the human subject find the nutriment necessary for the development of the embryo in the uterus. Hence the extremely small quantity of yolk with which they leave the ovary, and their minute size; their diameter, in their most perfect condition, being scarcely so much as one-tenth of a line. In their relation to the ovary, also, they differ in many particulars from the ova of oviparous animals. Owing to their extreme minuteness, the ovula of man and mammiferous animals for a long time escaped observation. Prevost and Dumas had remarked, that the ova found in the oviducts of animals, shortly after impregnation had taken place, were much smaller than the follicles of Graaf; and in two instances they actually saw the ovulum within the Graafian follicle, but they did not pursue the subject any farther. The merit of discovering the ovulum of mammiferous animals and man really belongs to Von Baer.

The vesicles or follicles of Graaf, or the ovicapsules which contain the ovula of mammals and the human subject, are connected together by a very firm stroma, which, with them, constitutes the ovary. They are but slightly prominent above the surface of the ovary in most Mammalia, but in the Ornithorhynchus are raised on pedicles as in birds. Each capsule is formed of two membranes, the more internal of which is like the ovicapsule of oviparous animals, lined with epithelium (membrana granulosa of Baer). The ovulum occupies only a very small part of the cavity of the Graafian vesicle or capsule, the remainder being filled with an albuminous fluid in which microscopic granules float. (See fig. 156, and fig. 153, page 1466.) In immature capsules the ovulum is proportionally larger and lies more nearly in the centre; while in those which are fully formed it is placed close to the inner wall of the capsule,

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portion of the albumen; 6, boundary of the most dense albumen; 7, the chalazæ; 8, the yolk; 9, the yolk-cavity; 10, the canal or duct leading to the cicatricula 11, cumulus proligerus; 12, the germ.]

* [According to Mr. Town (Guy's Hospital Reports, vol. iv. p. 390), there is a second delicate membrane within the well-known membrana testæ. The two layers of the latter are adherent throughout; and the folliculus aeris is formed by the newly-described membrane alone separating from it and passing directly across at the large end of the egg.]

Fig. 156.*

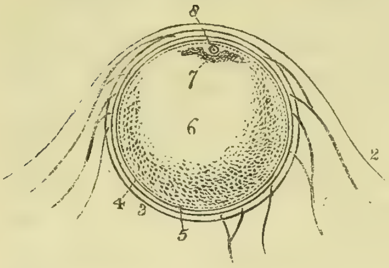


Fig. 157.†

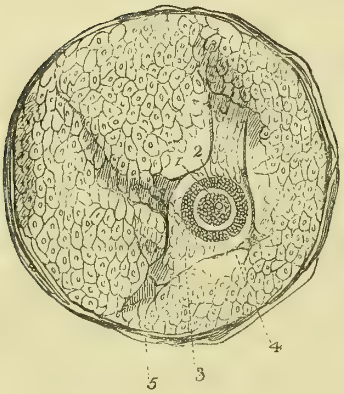
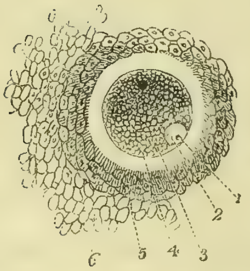


Fig. 158 ‡



imbedded in a granular zone (fig. 156 ^{7}). In both conditions, however, according to Barry, the ovulum is attached to the parietes of the follicle by peculiar granular bands or *retinacula* (fig. 157). In order to examine an ovulum, one of the Graafian vesicles, it matters not whether it be of small size or arrived at maturity, should be pricked and the contained fluid received upon a piece of glass. The ovulum then, being found in the midst of the fluid by means of a simple lens, should be placed under the compound microscope. Owing to its globular form, however, its structure cannot be seen until it is subjected to gentle pressure under a second thin lamina of glass, or by means of a compressorium.

The external investment of the ovulum is a thick membrane, which, under the microscope appears as a bright ring (fig. 158 ^{3}), bounded externally and internally by a dark outline. This membrane is called by Valentin and Bernhardt, *zona pellucida;* by R. Wagner, chorion. The anatomists who have occupied themselves most with the examination of this part of the ovulum, are divided in their opinions respecting its nature. According to Krause, it is composed of an albuminous mass, enclosed in a delicate membrane; while Wagner and Bischoff regard it as a simple tunic, because it tears with a uniform margin. Schwann admits that such is the character of its edge when torn, but nevertheless inclines, as does Dr. Barry§ also, to Krause's opinion.

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* [Graafian vesicle of a Mammal, after Von Baer. 1, Stroma of the ovary with blood-vessels. 2, Peritonæum. 3, External coat; and 4, internal coat, of the Graafian vesicle. 5, Membrana granulosa (of Baer). 6, Fluid of the Graafian vesicle. 7, Granular zone or disk, containing the ovum (8), and regarded by Barry as identical with the "retinacula" shown in fig. 157.]

† [Ovum of the Rabbit in the Graafian vesicle, after Barry. 1, The ovum, with its thick tunic or zona pellucida. 2, The tunica granulosa (of Barry). 3, The retinacula. 4, Cavity of the vesicle of Graaf, seen through an opening in the membrana granulosa of Baer, which lines the vesicle. 5, Coats of the Graafian vesicle.]

‡ [Ovum of the Hog, after Barry. 1, Germinal spot. 2, Germinal vesicle. 3, Yolk. 4, The broad zona pellucida or tunic of the yolk-sac. 5, The tunica granulosa of Barry, formed of a dense layer of granules similar to those contained in the fluid of the Graafian vesicle, and also to those which compose the membrana granulosa of Baer, and the "retinacula" of Barry. 6. Adherent granules.]

§ [According to Dr. Barry, the zona pellucida is a solid transparent membrane. He

Within this transparent investment lies the yolk, which consists of granules or cells and fat globules. This substance forms a globular mass which is usually in close contact with the inner surface of the investment above described. But sometimes in ova, which have attained the most perfect maturity, an interval can be seen between the yolk and its outer tunic, and this interval is rendered greater by the imbibition of water; so that it would seem probable that the mass of yolk is invested with a special membrane-like layer of granules.

For a long period after the existence of the germinal vesicle in the ova of oviparous animals was generally known, it remained undiscovered in the ova of mammiferous animals and man; and it then appeared doubtful, whether the ovula of the latter animals should not be regarded as analogous to the germinal vesicle of the oviparous classes. The germinal vesicle of the ovulum of Mammalia was first discovered by Coste, in 1834, but we owe the most accurate information respecting it to the researches of Valentin and Bernhardt. The vesicle is of largest relative size in the least advanced ovula. Its diameter is about $\frac{1}{60}$ of a line. The germinal vesicle can be seen while yet within the ovulum, if the latter be flattened by cautious pressure; and sometimes the ovulum may by the same means be ruptured, so as to allow the germinal vesicle to escape uninjured. Within the germinal vesicle, and close to its surface, is the germinal spot of Wagner, the diameter of which is no more than $\frac{1}{200}$ or $\frac{1}{300}$ of a line. The germinal spot is somewhat opaque, the rest of the contents of the vesicle transparent.

The discus proligerus does not exist in the ovulum of Mammalia, at least not with its characteristic form. But R. Wagner imagines that its place is here supplied by the continuous layer of granules which surrounds the entire yolk.

According to Carus, all the essential parts of the ovulum can be detected in the ovary of the mature embryo of the human subject, or of mammiferous animals. [See the Appendix for the most recent information on the subject of this Chapter.]

CHAPTER IV.

OF THE SEMEN.*

Great as are the advances which our knowledge of the ovum and female germ has made during the last few years, they do not surpass those

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states, however, that internal to this there is a much thinner membrane (the true membrana vitelli), which exists while the ovum is contained in the ovary, but disappears by liquefaction in the Fallopian tube, at the same time that the chorion begins to be formed. See Dr. Barry's Researches on Embryology, 2nd series, p. 322, 333, and 339.]

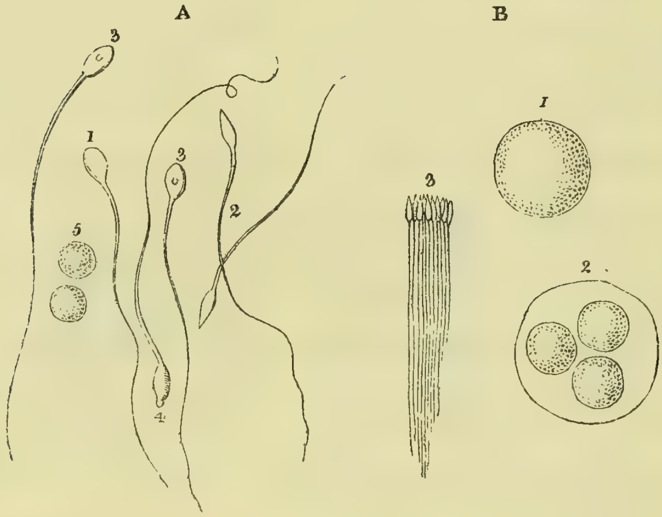
* *Bibliography.* Leeuwenhoek, Anatomia seu interiora rerum. Lugd. Bat. 1687. Arcana naturæ. Delphis, 1695. Epistolæ physiologicæ. Delphis, 1719. Gleichen, über die Samen und Infusions-thierchen. Nürnberg, 1778. Prevost et Dumas, Ann. des

by which our acquaintance with the fecundating fluid of the male has arrived at its present state of perfection. The semen has been made the subject of minute investigation by many anatomists, but with most success by Wagner and Von Siebold.

The ova or germs of the female are formed at a very early period, even in the embryo; but the semen and its essential elements are generally not present until the time of sexual maturity.

The semen of animals is a thick white or yellowish white fluid, having a peculiar penetrating smell. It becomes more transparent when exposed to the air, and is coagulated by alcohol; but its chemical properties are, with reference to the theory of generation, less important than its vital endowments.* It is composed of three distinct elements, a fluid, granules, and animalcules—the *spermatozoa.* These animalcules are found both in the vas deferens and in the vesiculæ seminales. The fluid of the semen cannot be obtained separate from its other components, and consequently its peculiar properties cannot be ascertained. The granules of the semen (see fig. 159 and 161) are described by Wagner as round bodies finely granulated on their surface, and measuring from $\frac{1}{300}$ to $\frac{1}{400}$ of a line in diameter; they must not be confounded with

Fig. 159.†



Sc. Nat. t. i. ii. Czermack, Beiträge zur Lehre von den Spermatozoen. Wien, 1833. Treviranus in Tiedemann's Zeitschrift für Physiol. V. pt. 2. Von Siebold in Müller's Archiv. 1836, p. 232, 1837, p. 381. R. Wagner in Abhandl. der K. Baiersch. Acad. 2. 1837, and Müller's Archiv. 1836, p. 225. Valentin, Repertor. 1836, p. 277. Dujardin, Ann. des Sc. Nat. t. viii. 291. 297. Donné, L'institut, 1837. 206. Ehrenberg, Die Infusions-thierchen, p. 464. [Valentin, Nov. Act. Nat. Cur. t. xix. Hallmann, Müller's Archiv. 1840. p. 467.]

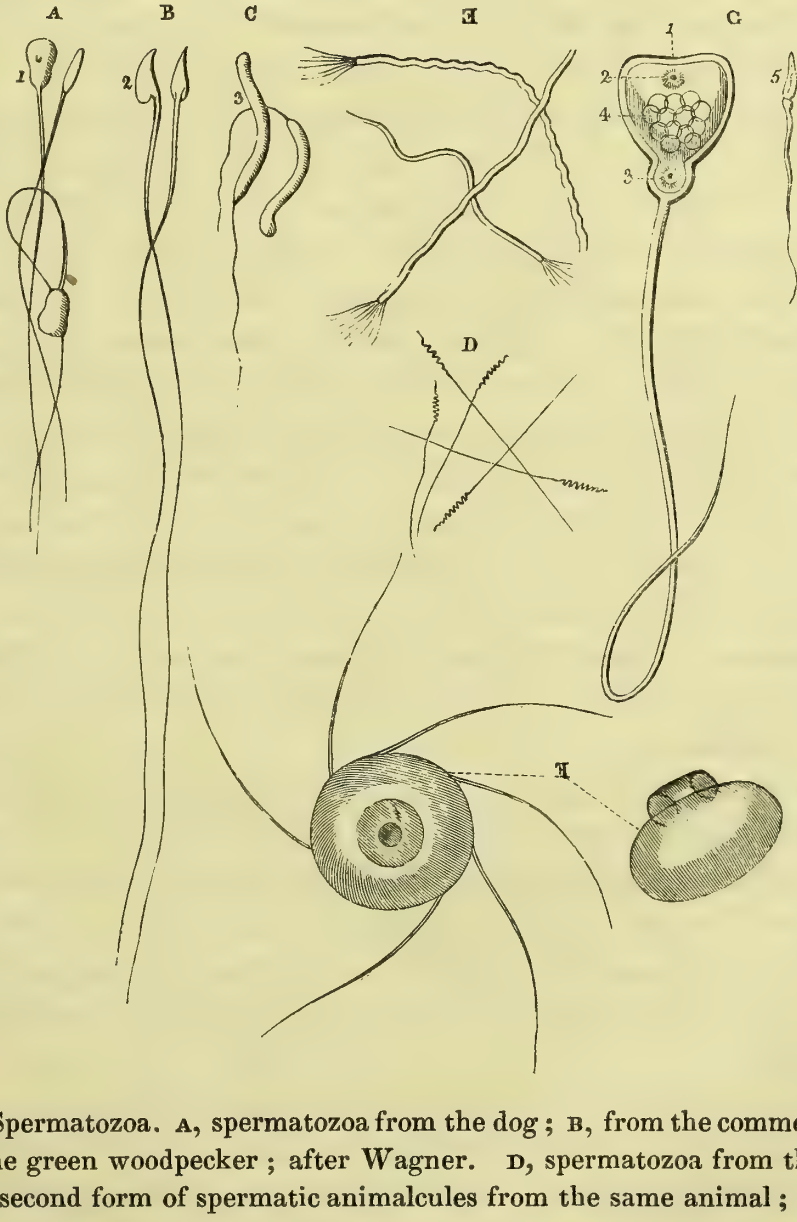
* See Berzelius, Thierchemie.

† [Spermatozoa of the human subject and their development. A, from the semen of the vas deferens. Spermatozoa fully developed; 1, with the surface depressed and smooth; 2, more acute and narrow; 3, with a circular spot in the middle of their flat surface, regarded by some observers as a sucker; 4, with a nodular process at their anterior extremity, not unlike a proboscis. B, from the semen of the testis. 1, large round corpuscules; 2, cells containing three granular roundish bodies, from which fasciculi of spermatozoa are developed (see page 1476); 3, fasciculus of spermatozoa, showing the mode in which they are grouped together in the testis. After Wagner.]

the particles of epithelium which are sometimes mixed with the semen. The spermatozoa, which were discovered by a student at Leyden named Ham, and first described by Leeuwenhoek, have different forms not only in different classes of animals, but also in different families, genera, and species. Their most remarkable varieties in the Vertebrata have been investigated and described by Wagner; in the Invertebrata, by Von Siebold. They are as follow:—

A few principal types may be distinguished: 1, animalcules, with an elliptical body and long caudal filament, like those of the human subject (fig. 159), and most Mammalia; 2, animalcules with pear-shaped bodies and caudal filament (fig. 160, A), which is their form in many other Mammalia; 3, animalcules with cylindrical body and caudal filament (fig. 160, C), a form met with in several birds, reptiles, amphibia, and fishes; 4, animalcules with a spirally twisted body and a caudal filament (fig. 160, D, and 161), such as exist in the singing birds, sharks, and paludinæ; 5, animalcules with the whole body filamentous or hair-like, as in many mollusca, insecta, and annelida.

Fig. 160.[*]



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[*] [Various forms of Spermatozoa. A, spermatozoa from the dog; B, from the common mouse; and C, from the green woodpecker; after Wagner. D, spermatozoa from the Paludina vivipara; E, second form of spermatic animalcules from the same animal; F, bodies contained in the semen of Astacus fluviatilis; after Siebold. G, spermatozoon of the bear, after Valentin: 1, anterior margin excavated; 2 and 3, two very dark circular spots regarded by Valentin as the mouth and anus; 4, a number of delicate circles, supposed by Valentin to be the outlines of gastric vesicles, of an hepatic organ, or of the convolutions of an intestinal canal. 5, the same animalcule, less highly magnified and viewed laterally.]

The spermatozoa of the human subject measure, according to Wagner, from $\frac{1}{50}$ to $\frac{1}{40}$ of a line in length; their oval flattened body from $\frac{1}{800}$ to $\frac{1}{600}$ of a line. The tail is at its commencement so thick that its two borders can be distinguished; but towards its free extremity it becomes of extreme tenuity. The spermatozoa of most Mammalia are of the same form as those of the human subject, but are generally larger, especially in the smallest animals, for example, in those of the mouse kind; their length in the rat being, according to Wagner, $\frac{1}{12}$ of a line. In monkeys they have great similarity to those of the human semen. In the dog, rabbit, and roebuck, the animalcules have a pear-shaped body. Their form is peculiar in the mouse kind, the extremity of their body being bent upwards and backwards like the point of a bellied bistouri or scalpel (fig. 160, B). In several Rodentia, as the squirrel, the body of the animalcule has its margin bent or rolled up. In birds, Wagner observed two forms of spermatozoa. The singing birds have spermatozoa with the anterior portion pointed and spirally twisted; the gallinaceous, predaceous, climbing and wading birds have animalcules with a narrow, straight, cylindrical body and short tail. The spermatozoa of the lizards, serpents, and frog, have a globular body and a delicate caudal filament; but those of the Salamandrina are differently shaped; in the Salamandra maculata, namely, the body tapers anteriorly to great tenuity, but ends with a knot. In the Tritons or water Salamanders the body of the animalcule is still less distinguished from the tail. The appearance of ciliary motion which has been observed on their tail, has been shown by Von Siebold to be due to the motions of the extreme portion of the caudal filament, which is bent back and wound in a spiral manner around the more anterior portion. The spermatozoa of the osseous fishes have a globular body; those of the cyclostomatous fishes a cylindrical one.

The spirally twisted form of the body of the seminal animalcules is rare amongst the Invertebrata. Siebold observed it in the Paludinæ. It is also seldom that the animalcules of the Invertebrata have an anterior much thicker portion or body, though this occurs distinctly in the bivalve Conchifera, and in a less marked degree in some Gasteropoda. Most commonly the spermatozoa of invertebrate animals are filiform.

The filiform spermatozoa of Insecta, Gasteropoda, and Distomata, are affected in a peculiar manner by water. Von Siebold observed that as soon as water was brought into contact with them they became twisted on themselves so as to form single or double loops.

With the organisation of the spermatozoa we are at present quite unacquainted, and it has hitherto appeared doubtful whether they have an animal organisation. Henle and Schwann perceived a spot in the body of the human spermatic animalcule, which called to mind the sucker of the Cercariæ; but this might have been a part, bearing the same relation to the body of the animalcule as the nucleus does to the cell. In many spermatozoa there is sometimes a small knot in the middle of the tail or towards its end; I observed this knot in the spermatozoa of Petromyzon marinus, but in most of the animalcules it was absent. Similar knots in the course of the caudal filament have been observed by Meyen in the spermatozoa of plants; for example, in those of Charæ.*

The movements of the spermatozoa resemble in their characters the voluntary motions of animals. They consist in lashing, undulating, and vibrating motions of the tail. Those with the spirally-twisted body have a corresponding spiral twisting motion.† In order to see their motions well, it is necessary to dilute the semen with serum of blood. In many instances these motions of the spermatozoa continue during many hours after the death of the animal from which they are taken, and the mode of its death has no influence upon them. Wagner observed the motions of the animalcules to cease soonest in the semen of birds; sometimes they did not continue more than fifteen or twenty minutes after the death of the bird to which they belonged. In the semen of Mammalia the animalcules in many cases continued to move for twenty-four hours, and in that of Amphibia and fishes still longer. High and low temperatures cause the motions to cease; Wagner, however, saw them continue in the spermatozoa of frogs and fishes when the temperature was below 32° F. The spermatozoa will live, according to Donné, in blood, milk, or mucus. Their death when mixed with saliva or urine, which Donné observed, must have arisen from other accidental circumstances; for Lampferhof observed them to continue their motions for a long period in saliva, and Wagner makes the same statement with respect to urine. In very acid mucus of the vagina, or very alkaline mucus from the uterus, they very quickly die, according to Donné's observation. Strychnine is stated by Wagner to kill them instantaneously; while, as we know from the researches of Purkinje and Valentin, the movements of the cilia of mucous membranes, and other surfaces, are not affected by narcotics.

The mode of development of the spermatozoa has been discovered by Wagner. During the winter the fluid of the testes of passerine birds contains merely small granules. In the spring there are granules of various forms, and, mingled with them, spermatozoa united in fasciculi. These fasciculi of spermatozoa are at first enclosed in very delicate vesicles or cells, in which they lie, all with their spirally-twisted anterior portions or bodies together at one end of the fasciculus, and with their caudal extremities at the other end. The animalcules in the testis present no motion, but in the vas deferens the individual animalcules are free and in motion. The semen of the testis contains, besides small granular globules, large vesicles, including one or two granular globules, and similar larger vesicular bodies, enclosing several such granulated globules. These vesicles have a close relation to the development of the spermatozoa; for Wagner observed that a finely granulated matter was at length deposited between the globules which they contain; that these globules then disappeared; and that a linear arrangement of granules began to be visible, which at length assumed distinctly the form of the fasciculi of spermatozoa above described (see fig. 161). The process of development of the spermatic animalcules is the same, according to Wagner's observation, in frogs and Mammalia (see fig. 159). In birds the spermatozoa are produced anew each year, and disappear in the autumn. In Mammalia their formation commences at an early age; in rabbits their development is completed, according to Wagner, at the third month after birth; in cats and dogs it is effected much later,

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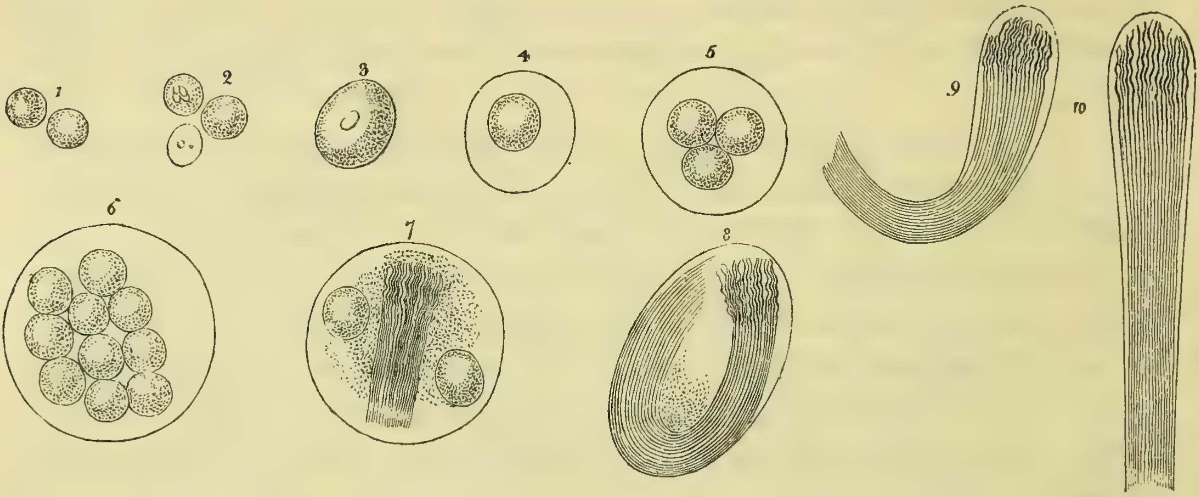
* [The spermatozoa which present the most evident signs of organisation are those of the Bear, described by Valentin (Nov. Act. Nat. Cur. t. xix). They appeared to him to have a mouth, an anus, and stomachs or a convoluted intestine. See fig. 160, G, at page 1473, and the explanation of that figure.]

† See Wagner's Physiologie, p. 15.

Fig 161.*



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* [Development of the spermatozoa of Certhia familiaris (the common Creeper); after Wagner. 1, Granules of the semen, granula seminis, obtained from the testicle when very much reduced in size during the winter; 2 to 10, different bodies found in the semen, taken from the testicle when very turgid during the summer; 2, 3, granula seminis, of which many are probably merely cells of epithelium; 4, 5, 6, cysts, or vesicles, containing one or several round granular globules; 7, a similar cyst, in which are seen, besides two globules, a mass of granules, and in this mass a fasciculus of spermatozoa in the process of development; 8, a similar cyst, become oval in form, while the spermatozoa have enlarged and are curled up within it,— the cyst still contains granular matter; 9, 10, cysts and fasciculi of spermatozoa still further developed; in 10, the fasciculus is ready to divide into separate animalcules.]

and in the human subject it does not take place until the period of puberty. These important observations have been confirmed by Von Siebold,* and Valentin,† [and by Dr. Hallmann,‡ who has observed the development of the spermatozoa in the cells of the testis of the ray.]

It is remarkable that in some animals (the number of which, however, is very small) no animalcules have hitherto been discovered in the spermatic fluid, even at the pairing season. The genus Astacus among the Crustacea presents this anomaly. In the river crab (Astacus fluviatilis) Henle and Siebold found, in place of the spermatozoa, peculiar motionless bodies, resembling large vesicles, with a smaller more opaque portion projecting from one side and with long hair-like filaments attached at different points of their surface (see fig. 160, F). Valentin has observed similar bodies in the seminal fluid of the lobster.

It is yet a question which cannot be answered with certainty, whether the spermatozoa are independent parasitic animals, or merely animated particles of the organism in which they exist. Ehrenberg is inclined to regard the spermatozoa as distinct animals, and places them with the Cercaria in the class of the true Entozoa. Treviranus, on the contrary, adopts the opposite view, and compares the spermatozoa to the grains of pollen. The absence of spermatozoa in the semen of some animals, and the existence of perfectly organised animals in the seminal reservoirs of the Sepia,§ are circumstances favourable to the former opinion: while, on the other hand, the absence of structure, such as other individual animal organisms possess, in the body of the spermatozoa; their presence in nearly all animals, and reappearance in almost the same form in the male generative organs of some plants; the fact of their being developed in a uniform manner from cells, and not from other spermatozoa; and the analogy which may be perceived to subsist between them and other organic cells, particularly the cells bearing cilia;

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* Müller's Archiv. 1839, p. 436.

† Repertorium, 1837, p. 143.

‡ Müller's Archiv. 1840, p. 467.

§ See the account of these bodies given by Carus in the Nov. Act. Nat. Cur. t. xix. p. 1; also Philippi in Müller's Archiv. 1839. [Carus imagined that these bodies were distinct animals, and described their large intestine, small intestine, stomach, proventriculus, and œsophagus. It has, however, been clearly shown by Von Siebold (Beiträge zur Naturgeschichte der Wirbellosen Thiere, Dantzig 1839), that Carus was in error, and that the original description given by Needham was, as far as it went, perfectly correct. They are really capsules containing the semen of the Cephalopod. The spongy mass, believed by the English microscopist to contain the semen, is, according to Siebold, composed almost entirely of spermatozoa, which have an oblong body, and long thread-like tail. Needham's observations were made on the Loligo; Siebold's on the Cyclops. Their views have been confirmed by Peters (Müller's Archiv. 1840, p. 98), and by Mr. Owen, in his Lectures at the Royal College of Surgeons, 1840. (See Lancet, May 14, 1840).]

are all circumstances opposed to that opinion. The spermatozoa resemble the cells bearing cilia, in their motions continuing after they are separated from the parent organism; and their caudal filaments may be compared to the cilia, while the nucleus of their body finds its analogue in the nucleus of the ciliated cells. In the character of their movements, however, the spermatozoa do not at all resemble the cilia, but present much more resemblance to animals moving voluntarily.

The most weighty argument against the special and individual animality of the spermatozoa is, their close connection with the fecundating property of the semen. Not only are they absent from the semen of many animals, and particularly of birds, except at the pairing time, but their development is imperfect in hybrid animals, which are generally incapable of reproducing their kind, or at most pair with individuals of one of the unmixed species, and produce forms which then return to the original fixed type. Hebenstreit, Bonnet, and Gleichen, all failed to detect spermatozoa in the semen of the male mule. More recently Prevost, and Dumas,* and R. Wagner, have examined the seminal fluid of hybrid birds, and have found the spermatozoa either absent or imperfectly developed. This fact of the spermatozoa being imperfectly developed in such animals is most important. In hybrids of the goldfinch and canary, the testes sometimes remain very small, but sometimes attain somewhat more than half the volume of those of birds of the parent species. In the latter case, the fluid of the testes is imperfect, as respects the spermatozoa and their germinal cells. In it Wagner found a few vesicles containing opaque molecules, and filaments enlarged at one extremity; but these filaments were never united in regular bundles, were not in normal number, and lay without regular arrangement, interspersed amidst the molecules. Such imperfectly developed spermatozoa remain of smaller size than those of the species which have produced the hybrid animal; their larger extremity is irregular in figure, is sometimes wedge-shaped, generally elongated, or curved at the point, but never twisted into the characteristic spiral form. In female hybrids Wagner† found numerous yolks with their germinal vesicles in the ovaries, but these ova never showed themselves advancing towards maturity.

Spermatozoa are sometimes met with in the male sexual organs of plants, but much more rarely than in animals. It being very difficult to distinguish the motion which the contents of the pollen grains of the higher orders of plants present from the molecular motion of Brown, we shall notice merely the spermatozoa of the Cryptogamic plants. Some phenomena referrible to spermatozoa of plants were observed by

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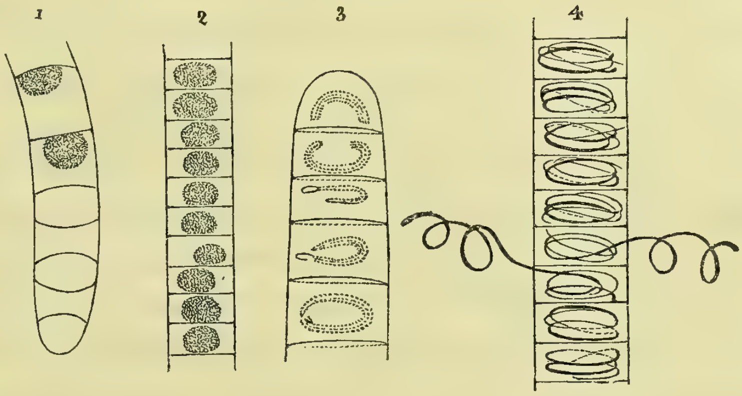
* Annal. des Sc. Nat. i. p. 183.

† Physiologie, pp. 25, 26.

Schmiedel and Fr. Nees Von Esenbeck. Unger first examined more closely the spermatozoa of the Sphagna, and it is to him and Meyen that we owe the most detailed information on the subject. The contents of the anthers of Sphagna consist of cells, each of which contains a filament, with a somewhat elongated ellipsoid head, rolled up in a spiral form. These thread-like animalcules move while still within the cells, escape from them, and then continue their motions. Meyen describes them as he observed them in the genera Hypnum, Mnium, Phascum, Polytrichum, and Sphagnum.* The spermatozoa in the cells of the anthers of the Hepaticæ, for example, of Marchantia and Jungermaneria, present, according to the observations of Meyen, similar appearances.

The spermatozoa of the Chara† are developed in articulated filaments found in the anthers, and connected with them. In each of the series of cells which form the articulated pollen thread, a globular cell of a mucous substance is developed (1, 2), and in the interior of each of these cells a single spermatic animalcule. At first the animalcules are shapeless (3); in cells further advanced in development they can be seen to be spirally convoluted, but are still motionless; and in others still nearer to maturity they present an active rotatory motion (4). If these animalcules are watched under the microscope they can be observed to break through the wall of the cell in which they were contained, and to issue with their larger end forwards. Professor Meyen has had the kindness to show me all the steps of this process with the aid of the microscope. These animalcules of the Chara are of very great length, so that, except in the convoluted state, they could not be contained in

Fig. 162 ‡



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* Compare Unger, Nov. Act. Nat. Cur. t. xviii. pt. 2. p. 785.

† They were first well described by Varley. The most complete account of the spermatozoa of plants will be found in Meyen's Pflanzen-physiologie, p. 218. Tab. xii. fig. 17—28.

‡ [Filaments of the anthers of Chara Vulgaris with spermatozoa in different stages of development, after Meyen. 1, a filament, in which only two of the mucous cellules are yet formed; 2, a filament, in which a cellule has been developed in each compartment; and in the filament 3, the formation of the spermatozoa in their mucous cellules is commencing; and in the last filament, 4, their development is complete, and two are escaping from the compartments which contained them.]

their cells. When they have escaped into the surrounding water they move with their thin thread-like extremity foremost. In their form they resemble the intestinal worm Tricocephalus, being thicker at one end and tapering gradually into an extremely long filament. The thicker part is spirally twisted, while the threadlike part assumes in its energetic motions various positions. These spermatozoa live many hours after their escape from the cells of the pollen threads.

CHAPTER V.

OF PUBERTY, SEXUAL INTERCOURSE, AND FECUNDATION.

I. *Puberty.*

The period of puberty, the commencement of that part of life which is distinguished by the capability of propagating the species, does not occur exactly simultaneously in the two sexes; and still greater variety in this respect is caused by differences of nation and climate. Puberty declares itself in the female sex of our climate about the 13th, 14th, or 15th year, and is indicated by the occurrence of menstruation. In the male sex puberty commences about the 14th, 15th, or 16th year, and is attended with the secretion of semen, and with the occurrence of discharges of that fluid. In hot climates the body undergoes the changes of puberty earlier than in cold climates. It is stated that in the hot regions of Africa they take place in the female sex as early as the 8th year, and during the 9th year in Persia. Young Jewesses are also said to menstruate earlier than other females in our own country. The capability of reproduction generally ceases in the female sex, together with the function of menstruation, between the 45th and 50th years. The duration of the reproductive power in man cannot be so exactly defined; in general, it continues longer than in woman; and not unfrequently very old men manifest a remarkable degree of virile power.

The changes in the system which characterise the period of puberty are partly local, affecting the generative organs, and partly of a general nature. The local changes consist in the growth of hair on the pubes in both sexes; in the menstruation of the female; in the copious formation of semen, and occurrence of erection in the male; and in the enlargement of the breasts in the female sex. The general changes of the system affect principally the respiratory and vocal apparatus, the entire form of the body and the physiognomy, the character of the mind, and the feelings relating to the sexes. The respiratory organs acquire an increase of volume at the age of puberty, especially in the male sex; and the vocal apparatus undergoes those changes of dimensions and acoustic properties which have been described at another part of this work (see page 1031). The whole body attains its most perfect form; while the features receive their stamp of individuality, and present signs of serving to express the passions, though they are not yet so strongly marked as in many adults. Sexual ideas arise instinctively and obscurely in the mind, and set in action the creative power of the imagination; but, at the same time, by their influence on the whole mind, call into play the noblest mental faculties, so as to elevate and adorn the feeling of love.

Menstruation is the periodical discharge from the female generative organs of a bloody fluid poured out by the inner surface of the uterus. The first discharge is usually preceded and accompanied by some symptoms of general disturbance of the system, namely, by abdominal congestion, pain in the loins, and a sense of fatigue in the lower limbs. Its periodical return is also attended in most women by abnormal symptoms, which are different in different individuals. The menstrual periods occur usually at intervals of a solar month; their duration being from three to six days. In some women the intervals are as short as three weeks, or even less; while in others they are longer than a month. Aristotle* made the extraordinary statement that menstruation rarely occurs every month, but in most women only every three months.

The menstrual discharge differs from ordinary blood in no other respect than that of containing only a very small quantity of fibrine, or none at all.† The blood corpuscules exist in it in their natural state.

Menstruation does not occur in pregnant women, nor in most cases in those who are suckling. But in rare instances it continues even during pregnancy.

Menstruation, in the strict sense, is peculiar to the human female. A kind of menstrual discharge was occasionally noticed by Rengger in the female of Cebus Azarræ; but this did not occur at regular periods. It was small in quantity, continued two or three days, and returned after intervals of three, six, or even ten weeks. This sign of maturity did not show itself until the end of the second year.‡ Geoffroy St. Hilaire, and Fr. Cuvier,§ have observed many facts of a similar kind among the monkey tribe. They noticed discharge of blood with enlargement of the sexual organs in Cercopithecus, Macacus, and Cynocephalus; but they maintain that these appearances were coincident with the monthly heat. During the periodical sexual heat in other animals also, as the horse and dog, there is sometimes a discharge of blood. But the menstruation of the human female is a phenomenon of a totally different nature, and has no connection with sexual excitement.

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* Hist. Anim. 7. 2.

† Lavagna, Meckel's Archiv. 1818, bd. iv. p. 151.

‡ Rengger, Naturgeschichte der Säugethiere von Paraguay. Basel. 1830, p. 49.

§ See their work, Hist. Nat. des Mammifères. See also Ehrenberg, Abhandl. der Acad. zu Berlin. 1833, pp. 351—358, on the occurrence of menstruation in the monkey tribe; and Numan, Froriep's Notizen, p. 150, on menstruation in animals generally.

We are quite ignorant of the cause of menstruation and its periodical return. The notion of the ancients that it cleansed the body from noxious matters is evidently erroneous. The opinion, also, that its office is to relieve the uterus of the blood which during pregnancy would nourish the embryo, is unsatisfactory, since the small quantity of blood lost in menstruation does not correspond with the amount of nutriment which the fœtus derives from the mother. More probability attaches to the view that the human female is preserved from too great sexual excitement by the menstrual flux. But it is still more probable that menstruation is the result of a periodical regeneration,—a kind of moulting of the female generative organs, attended perhaps with the formation of a new epithelium. The periodicity of the phenomenon is not connected with the changes of the moon, but with some condition of the organism itself; like other periodical actions or functions, it has an internal cause. The variations of the light afforded by the moon bear no constant relation to the periods of menstruation; on the contrary, different females are menstruating on every day of the month. The intervals of menstruation also, even when most regular, are not lunar but solar months; and they are very different in different women, in consequence of the various states of their system, and quite independently of external causes. [For more recent information on the subject of menstruation, see the Appendix.]

In the male sex the tendency to periodicity is manifested only in the turgescence of the genitals, and greater excitability and potency of the spinal cord and nerves engaged in the generative function; a state which is terminated, as it were by a crisis, in the act of coïtus, or in the involuntary emission of semen. Women are much less, or perhaps not at all, subject to such periodical sexual excitement. The periodical heat occurs in the most marked degree in animals. In many of them it happens during the spring, as in most birds, reptiles, and Amphibia, in many fishes, and also in many mammals, as the rodents, moles, and horses. In other animals, as several fishes, birds, Amphibia, and Mammalia, the summer is the season of sexual heat; while in others again, as many ruminants, it occurs in the autumn; and in others, as dogs, cats, and other carnivorous animals, in the winter.* In tame animals the periodical sexual excitement is manifested with much less intensity than in the same animals in their wild state; and in many, as the elephant, sexual union never takes place while they are in confinement.

All the phenomena connected with the sexes which animals present, are dependent on the formative generative organs, the ovaries and testes, and on the influence which they exert on the rest of the organism. Not merely does castration during youth for the most part prevent the development of the sexual feelings and emotions; but even when performed at adult age, that operation destroys nearly entirely the sexual excitability. Sir A. Cooper* had the opportunity of knowing during twenty-nine years a man, both of whose testes had been extirpated. The operation was performed in 1801. "For nearly the first twelve months, he stated that he had emissions in coïtu, or that he had sensations of emission. That then he had erections and coïtus at distant intervals, but without the sensation of emission. After two years he had erections very rarely and very imperfectly, and they generally immediately ceased under an attempt at coïtus. Ten years after the operation, he said he had, during the past year, been once connected." In 1829 he stated, "that for four years he had seldom any erection, and then that it was imperfect. That he had for many years only a few times attempted coïtus, but unsuccessfully; that he had once or twice dreams of desire and a sensation of emission, but without the slightest appearance of it."

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* See the more detailed account in Burdach's Physiologie, bd. i. p. 381.

II. *The act of sexual union.*

The act of sexual union, as regards the male sex, consists of erection and the ejaculation of semen. Erection is the result of the arrest of blood in the corpora cavernosa of the penis, affected most probably, as Krause † shows, by the action of the musculi erectores penis, which compress the deep veins of the organ as they issue from the corpora cavernosa, though they can exert no influence on the vena dorsalis. In the horse the veins of the corpora cavernosa give off such numerous communicating branches in different directions, that it is more difficult to explain there the act of erection.‡ The part played by the arteriæ helicinæ in this act is not known; they cannot, however, be its sole cause, since in several animals, as the elephant, they do not exist, and even in the horse have quite a rudimentary form. It is in these animals that the muscle-like bands, passing between the veins of the corpora cavernosa, which were first observed by Hunter, are most highly developed. The remote source of the power of erection is the spinal cord; and hence the loss of this power in cases of Neuralgia dorsalis or Tabes dorsalis.

The emission or ejaculation of the semen is a reflex action excited by irritation of the sensitive nerves of the penis. The act of ejaculation is itself the result of two movements; namely, of the persistent contraction of the organic muscular fibres of the vesiculæ seminals, and of the repeated periodical contraction of the animal muscular fibres of the ejaculator seminis, and other perinæal muscles. Sudden irritation and injury of the medulla spinalis give rise to emission of semen, which is then not necessarily attended by erection. Discharge of semen is an ordinary phenomenon in decapitated criminals. That the vesiculæ seminales are really receptacles of semen is beyond a doubt, since spermatic animalcules have been discovered in their contents in the human subject after death. They are, therefore, not mere secreting organs as Hunter supposed.* Hunter, however, proved by a series of observations, that when one testicle is extirpated, the vesicula seminalis of that side does not undergo diminution in size; and his view respecting the office of the vesiculæ was correct, so far as regards their secreting a mucous fluid. In the act of coition, however, the semen comes directly from the vesiculæ seminales, and not from the testes. It is, moreover, mixed in the urethra with the secretion of Cowper's glands, and with that of the prostatic gland, of the nature of which we are quite ignorant.

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* On the structure and diseases of the testis, pp. 53, 54.

† Müller's Archiv. 1837.

‡ On the cause of erection in the horse, consult Guenther, Untersuchungen und Erfahrungen im Gebiete der Anatomie, Physiologie und Thier-arzneikunde. Hannover, 1837.

In both sexes the act of coition is attended with pleasurable sensations, but their respective share in the act itself is very different. In the female there is no expenditure of nervous power in the production of erection, no energetic rhythmic muscular contractions when the venereal excitement has reached its height, and no emission of semen; but merely an increased secretion of mucus from the mucous follicles of the vagina, excited by the impressions on the sensitive nerves of the female sexual organs, and serving to lubricate the passage. The man feels exhausted after the act; the woman does not. It appears, therefore, that the nervous excitement and actions of the male during the act of coition, attain, in a short period, a great degree of intensity, and are as rapidly depressed, while there is no evidence that such is the case in the woman. The clitoris, which is known to be the part most susceptible of the pleasurable sensations in the female, is not, like the penis of the male, rendered by friction the seat of intense sensation and nervous excitement during coition, and hence its excitability is found not to be wholly exhausted after the act is completed. We are, therefore, justified in concluding that the sensitive excitement of the woman is neither so rapidly rendered intense, nor so rapidly depressed, as that of the man; and this conclusion accords with the fact, that women bear frequent sexual intercourse better than men, and are much less frequently affected with Tabes dorsalis, in consequence of sexual excess. The clitoris, though agreeing with the penis in its mode of development, yet differs from it essentially in its functions, since it is generally incapable of true erection. In the genus of monkeys, Ateles, the clitoris is normally of extraordinary length, and this circumstance has given foundation to the accounts related of the structure and habits of some female monkeys. The clitoris of the females of the genus Ateles has very large corpora cavernosa, in which, however, I have found merely fat; while the sensitive nerves of the penis, the nervi dorsales, were very large.* This large size of the clitoris is peculiar to the genus Ateles; in other genera of monkeys the organ presents nothing unusual.

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* Hunter's works [Palmer's edition], vol. iv. p. 20.

III. *Separation of the ova from the ovary, and their reception into the Fallopian tubes.*

In oviparous animals the separation of ova from the ovarium may take place either independently of impregnation by the male, or as the result of that act. In the Amphibia, the ova of which are impregnated out of the body of the female, for example, in frogs, the ova have separated from the ovary, and have accumulated in the oviduct long before the time of fructification. The ova of the female frog having accumulated in the oviduct, and distended it to a considerable size, are expelled from it by the action of its walls during the excitement of copulation, and are immediately impregnated by the male, who sits on the back of the female, firmly embracing her.

In fishes, also, the ova seem to separate from the ovaries before fecundation. For in the majority of fishes there is no sexual union. The male and female, under the venereal excitement, accompany each other through the water, and the ova being deposited by the female are fecundated by the semen which the male emits. There are some fishes, however, as the Blennius viviparus and other viviparous fishes, in which internal impregnation is effected, either by the semen emitted by the male finding its way with the water into the internal generative organs of the female, or by an actual act of copulation as in the sharks and rays.

Birds, also, which begin to lay their eggs after copulation and impregnation, continue to lay them when they are kept quite separate from the male bird; and here, also, the ova evidently separate from the ovary, independently of impregnation. The same is the case with some insects, as, for example, butterflies; for they also deposit mature ova when they have been kept isolated from the male from the time of their entrance into the chrysalis state.

In Mammalia, on the contrary, the separation of the ova from the ovary seems to be dependent on the act of impregnation. It has, it is true been stated, that cicatrices of the ovaries, resulting from the escape of ova, have been seen in the bodies of virgins;* but that is certainly not an ordinary occurrence. Usually, it is only after a successful union of the sexes, that one or more Graafian vesicles are found turgid. At a somewhat later period, after coition has taken place, the turgid and vascular vesicle of De Graaf bursts, and the ovulum is received into the Fallopian tube. These results of a fruitful union of the sexes, the change in the condition of the ovary, the dehiscence of the Graafian follicle and escape of the ovulum, are now known to be consequences of the direct action of the semen on the ovary itself, and not of its action merely on the external generative organs. For Professor Bischoff and Dr. Barry have made the important discovery, that the semen of male mammiferous animals which have been induced to copulate, is really conducted through the entire length of the Fallopian tube to the ovary. [For an account of recent observations on the discharge of ova from the ovaries, see the Appendix.]

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* See Fugger, De Singulari Clitoridis in Simiis Generis Ateles Magnitudine et Conformatione. Berol. 1835.

The mode in which the ova, unimpregnated or impregnated are transferred from the ovary to the Fallopian tube or oviduct is far from being accurately known.

In Mammalia and birds, the proximity of the ovary to the infundibulum of the Fallopian tube must, to a certain extent, facilitate the entrance of the ovum into the latter; but even here there is a phenomenon, as yet unexplained, in the Fallopian tube applying its infundibulum, or fimbriæ, at the time of impregnation, not merely to the ovary, but exactly to that part of it at which there is an ovicapsule on the point of bursting. This erectile turgescence of the Fallopian tube, and its close application to the ovary, have been many times observed in mammiferous animals,— namely by De Graaf, Kuhlemann, Haighton, Cruikshank, Von Baer, and Wagner. The phenomenon continues during the first few days after coition has taken place. Von Baer observed it in pigs and sheep as late as the fourth week, while Wagner found that it ceased in pigs about the eighth or tenth day.

It is still more difficult to explain the passage of the ova into the Fallopian tube in those animals in which the infundibulum of the tube lies at a considerable distance from the ovary, as is the case in the Amphibia, and sharks and rays. In the Amphibia the infundibular extremity of the tube lies at the most superior or anterior part of the abdominal cavity, far above the ovary, and in the sharks and rays the disposition of the parts is apparently still more unfavourable to the transit of the ova into the Fallopian tubes; for in them these tubes terminate by a common orifice in the middle line, above the liver, and just beneath the diaphragm or septum, which separates the cardiac cavity from the abdomen, while the ovaries lie at the sides of the liver, or beneath it, in the middle line close to the vertebral column. It is very probable, that in these cases the motion of cilia on the surfaces between the ovaries and Fallopian trumpets effects the transit of the ova. The observation of Mayer, that the peritonæum of frogs presents the ciliary motion, is in favour of this view. Valentin informs me in a letter, that he has detected ciliary motion on the surface of the peritonæum, between the liver and ovary; and also on the peritoneal covering of the kidneys and ovaries in sharks. I learn also from C. Vogt, that the whole internal surface of the abdominal cavity presents the ciliary motion in the female salmon, a fish which has no oviduct, the ova falling into the cavity of the abdomen, and escaping from it by the simple openings already described (page 1461). The ciliary motion which exists on the inner surface of the Fallopian tubes and of its fimbriate appendages in Mammalia, must in them also have great influence in aiding the entrance of the ovum into the tube. Henle has discovered the existence of ciliate epithelium even on the outer surface of the fimbriæ in the human subject.*

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* Home, Philos. Transact.

The changes which precede the expulsion of the ovum from its capsule, and which the capsule afterwards undergoes, are the following:—Both in oviparous animals and in Mammalia the posterior part of the capsule swells before the escape of the ovum; but in Mammalia this tumefaction is much greater than in other animals, and the swollen capsule appears very vascular. Even before the ovulum has left its cavity, the capsule becomes in a great part filled with a brownish yellow substance. In consequence of this change the contents of the capsule are protruded against its outer wall, which has become thinner, and now projects with the ovulum beneath it in a hemispherical form above the surface of the ovary and thickened follicle. An aperture, the stigma, is then formed, at the most prominent point. Immediately after the escape of the ovulum the cavity of the follicle, or Graafian vesicle, appears very small; in a short time it becomes quite filled with a granular mass, and a kind of wart is developed in the situation of the former opening. This wart afterwards disappears, and then the altered follicle remains with the form of the round corpus luteum. In oviparous animals the calyx gradually diminishes in size after the escape of the ovum, and is retracted into the mass of the ovary and absorbed.

According to Dr. Barry,† the corpus luteum of mammiferous animals is developed in the vascular covering of the ovisac, or external tunic of the Graafian vesicle. Dr. R. Lee,‡ on the contrary, supposes that it is formed externally to both coats of the vesicle. [Dr. Montgomery * and Dr. Patterson,† again, state as the result of their observations, that the substance of the corpus luteum is deposited between the two coats of the follicle. The forms represented by this body at different periods after impregnation are shown in fig. 163.] The true corpus luteum appears never to be produced except as the result of conception. False corpora lutea, on the contrary, are frequently met with. They generally, according to Dr. Montgomery, appear to be formed by an extravasation within the Graafian vesicle. A thickened state of the coats of the vesicle, which ensues in advanced age, sometimes simulates a corpus luteum. False cicatrices of a vesicle have an irregular form, and want the small round opening which is the result of conception. In the ovaria of women who had died during menstruation, Dr. Lee saw other appearances which might have been mistaken for corpora lutea. The Fallopian tubes were red and turgid; the peritoneal coat of one ovary was perforated by a small circular opening, around which the surface of the ovary was elevated, and of a bright red colour, and the opening sometimes communicated with a cavity; but the distinctive characters of the corpus luteum were wanting. [More recent observations on the corpus luteum will be found detailed in the Appendix.]

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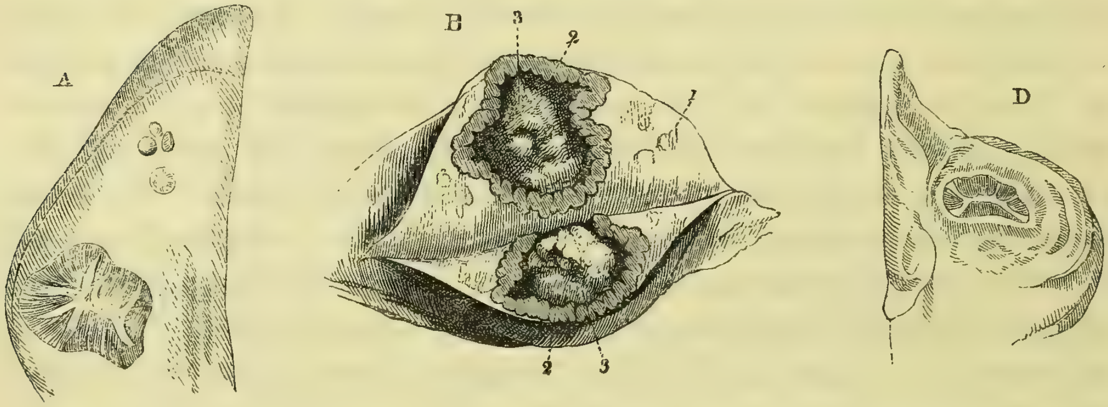
* Müller's Archiv. 1838, p. 114.

† Phil. Trans. 1839. Pt. ii. p. 317.

‡ Med. Chir. Trans. vol. xxii. p. 329.

Fig. 163.‡



IV. *Fecundation.*

The semen might be supposed to effect fecundation in different ways. Its immediate action might be on the organism of the female, the fecundation of the ovum being a secondary and indirect result of this action; or it might be exerted directly upon the ovum itself. In the former case, the semen could be conceived to act as a stimulant of the female genitals, producing a state of excitement of which fecundation is the effect; or it might be absorbed into the blood of the female, which would explain, not only the changes that take place in the ovary, but also the more general results of fecundation. There have, indeed, been writers who, resting on these theories, have imagined the possibility of fecundation being effected in other than the ordinary way, by means of semen infused into the blood. Observations, however, have shown that the fecundation, following union of the sexes, results from the direct action of the semen upon the ovum. This is proved partly by the experiments of Haighton,* in which ligature of one Fallopian tube before copulation prevented the impregnation of the ovary of that side, while fecundation always took place in the ovary of the opposite side on which the Fallopian tube was left free; and partly by the cases in which, either artificially or naturally, impregnation is effected quite independently of the female organs of generation. The ova of frogs are naturally impregnated independently of the genital organs of the female, the semen of the male being shed upon them after their expulsion. The experiment of the artificial impregnation of the ova taken from the body of female frogs, by means of semen from the testicle or vesicula seminalis of the male frog, has been well known since the time of Spallanzani. In this experiment fecundation takes place if the ova and semen are brought into immediate contact, but is prevented by the interposition of a thin but impermeable medium, such as taffeta. The experiment succeeds in the case of these cold-blooded animals, even when the male and female individuals from which the semen and ova are taken have been dead several hours. Rusconi † has recently performed similar experiments on artificial impregnation with the ova of fishes, and with the same results.

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* On the Signs of Pregnancy, p. 216.

† Edinb. Med. and Surg. Journal, Nos. 142 and 145.

‡ [Corpora lutea of different periods. B. Corpus luteum of about the sixth week after impregnation, showing its plicated form at that period. 1. Substance of the ovary 2. Substance of the corpus luteum. 3. A greyish coagulum in its cavity; after Dr. Patterson. A. Corpus luteum, two days after delivery. D. In the twelfth week after delivery; after Dr. Montgomery.

It is equally certain that fecundation does not depend on any influence of the entire male organism, but on the semen alone. This, indeed, was proved long since by experiments of Spallanzani and Rossi, who found that semen of a dog, introduced by means of a syringe into the generative organs of a bitch, effected impregnation. There can therefore, be no doubt that the essential cause of fecundation, wherever it takes place, is not any influence of the male organism upon the female, but the action of the semen itself upon the female germ.

Two views have been taken of the mode of action of the semen on the ovum. Some physiologists have believed it to be immediate, while others have supposed it to take place through the intervention of a peculiar emanation, the aura seminalis. The falsity of the latter opinion is sufficiently proved by Spallanzani's observations, already referred to, which show the necessity of absolute contact of the semen with the ova of frogs, for producing fecundation. Where the ova were suspended above the semen, and very close to its surface, no fecundation took place; while semen, diluted in the proportion of three grains to eighteen ounces of water, was efficient for impregnating by contact. Spallanzani found a drop of this fluid adequate to impregnate ova.*

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* Phil. Trans. 1797.

† Müller's Archiv. 1836, p. 278.

But it is not merely in Amphibia and fishes that the contact of the semen with the ova is thus necessary for fecundation; the fact of the semen being conveyed in Mammalia from the uterus along the Fallopian tubes, even to the ovary, proves that the same condition obtains in all animals. The semen passes into the uterus either soon after or during the act of copulation. Leeuwenhoek, on several occasions, detected spermatozoa in the uterus of mammiferous animals, which had recently had sexual union. Prevost and Dumas † discovered them in the uterus twenty-four hours after the act of copulation, and on the third and fourth days in the Fallopian tubes. Bischoff's observations‡ are still more conclusive. In a bitch which had had coition with a dog nineteen hours before, and again half an hour before it was killed and examined, he found spermatic animalcules upon and between the fimbriæ of the tubes. In a second instance, in which the examination was instituted forty-eight hours after coition had taken place, he detected the seminal animalcules not merely in the uterus and Fallopian tubes, but also on the ovary itself. In Mammalia, therefore, as well as in other animals, it is an ascertained fact, that the semen and ovum are brought into immediate contact.§

The situation in which the impregnation of the ovum takes place is very different in different animals. We have already seen that the ovum may be separated from the ovary before as well as subsequent to impregnation. Hence it follows, that impregnation may take place in three situations.

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* See Spallanzani, Expériences pour servir à l'Histoire de la Génération. Genève, 1786.

† Annal. des Sc. Nat. tom. iii. p. 119.

‡ Wagner's Physiologie, p. 49.

§ [Dr. Barry's observations were made on the rabbit. In seventeen out of nineteen instances he was unable to discover spermatozoa in the fluid collected from the surface of the ovary. On one occasion he found a single spermatozoon, which was dead, while the ova had escaped. On a second occasion he found, twenty-four hours post coïtum, several spermatozoa on the ovary. Some of these animalcules were alive and active, though not in locomotion; others were dead. There was no enlargement of the Graafian vesicles, nor a high degree of vascularity of any of the parts. Phil. Trans. 839, pt. ii. p. 315.]

a. *Impregnation external to the body of the female.*—It has already been mentioned, that this is the mode of impregnation in most Amphibia and fishes.

b. *Impregnation of the ovum while still in the ovary.*—This is the place of impregnation, at all events, in man and mammiferous animals. In all cases of extra-uterine pregnancy, in which the ovum is developed in the ovary itself, or escaping into the abdominal cavity is developed there, it cannot be doubted that the ovum was in those instances impregnated in the ovary; but the fact of Bischoff and Barry having traced the spermatozoa as far as the ovary, proves that impregnation is always effected in that situation in Mammalia. The mode in which the semen is conducted so far through the female generative organs, is no longer a problem requiring solution; for the discovery of the ciliary motion affords a solution of it. The rapidity with which matters are made to move over surfaces furnished with vibrating cilia, may be readily shown in the frog, by Dr. Sharpey's experiment. The lower jaw being cut away, powdered charcoal is strewn upon the palate, when it is perceived to move visibly and pretty rapidly in the direction of the fauces, and has frequently in a few minutes quite disappeared. The only point here which requires solution, respects the mode of introduction of the seminal animalcules into the uterus. This part of the process cannot be effected by the movement of cilia, for the mucous membrane of the human vagina presents no ciliary motion. Henle could detect no ciliary epithelium lower than the middle of the neck of the uterus. Still, notwithstanding the great narrowness of the orifice of the uterus in young females, we can conceive that the semen may be mechanically forced through it during the act of coition by the movements of the penis. It is difficult, however, to explain the occurrence of fecundation when the hymen is still perfect, or when the penis is very short or affected with congenital hypospadia. How fecundation is attained in these cases, which are rare, is quite a mystery.* I must, however, remark, that it is only in the first of them,—that of the persistent hymen, — that the possibility of fecundation appears to me to be absolutely certain. In other cases, all the conditions for absolute proof cannot possibly be fulfilled; for, that the impregnation of a female was effected by a hypospadiac and not by another man, must always be a mere matter of faith.

c. *Impregnation of the ovum in its passage from the ovary to the exterior of the body.* — Since the ova of birds separate from the ovary quite independently of fecundation, there is no difficulty in understanding that they may become fecundated not merely by the semen being conveyed along the walls of the oviduct to the ovary, but also by meeting the semen in their passage through the oviduct, as long as their yolk-sac is not surrounded by a layer of albumen and by the shell. In the case of the tritons, or water salamanders, no actual sexual connection takes place, but the male merely lashes the female with its tail, according to the observations of Spallanzani and Rusconi, while it emits the semen into the water; and here it is possible the semen may penetrate with the water into the generative organs of the female, which afterwards expels the ova and fixes them upon leaves. With respect to the viviparous species of oviparous animals, as the oviviparous sharks and rays, the Blennius viviparus, the Salamandra maculata, the viper, &c. (where the ovum, enveloped in a soft membrane, in place of a hard shell, is developed within the uterus or oviduct, though devoid of a placenta or other connection with the parent organism), it is uncertain whether fecundation takes place in the ovary itself or in the oviduct.

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* See the remarks on cases of this kind in Burdach's Physiology, bd. i. 528.

One of the most interesting varieties in the process of fecundation is presented by insects. Connected with the vagina of the female insect is a sac or capsule, which receives the semen during the act of coition, and in which seminal animalcules can be detected for a long period after that act. In consequence of this provision the ova can be successively subjected to the fecundating influence as they are expelled. No certain proof exists that such is always the process, and that the semen does not pass from this sac up the oviducts, and impregnate the ova successively in the ovary; and in insects, such as the Phasma, the ova of which, while yet in the ovarian tubuli, have a very firm shell, it would be very difficult for fecundation to take place, while the ova are being expelled. In many insects, however, the fact of the fertilisation of the ova in their transit through the excretory passages cannot be doubted. Thus, according to Von Siebold, in the Melophagus ovinus, the ovaries open into a receptacle which, in its turn, communicates with the uterus. In the act of copulation the receptacle, or spermotheca, becomes filled with semen; and, since the ova in their transit to the uterus pass through this receptaculum seminis, it is easy to understand how an insect, after one act of copulation, can produce a succession of living young.*

Of the intimate changes on which fecundation depends, we are yet wholly ignorant; and up to the present time it was the less possible for us to become acquainted with them, since we were uncertain even as to the situation in which the process took place. The principal question which it is desirable to decide with regard to the nature of the fecundating process respects the part which the spermatozoa play therein. Do they serve merely to increase the sphere of action of the fertilising matter, as insects, carrying abroad the pollen, aid in the fecundation of plants, or do they themselves contain the essential fertilising principle? The observation of R. Wagner, that the spermatozoa suffer a change of form in hybrid animals (see page 1478), is in favour of the latter view. The spermatic animalcules, however, certainly bear no intimate relation to the germinal vesicle; for in the ova of oviparous animals the germinal vesicle disappears at the time of their discharge from the ovary when they are yet unimpregnated. Equally certain is it that the spermatozoa do not become the future embryos. For the germinal disk appears perfectly unchanged after fecundation, and the development of the embryo by the growth of the germinal disk to form the germinal membrane, and the subsequent changes of organization, can be accurately traced.* Vegetable physiology has gone a step further than animal physiology in the elucidation of the act of fecundation; hence, it is important for us to examine this process as it occurs in the vegetable kingdom.

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* This subject has been very fully investigated by Siebold. Müller's Archiv. 1837, p. 381.

The parts of plants which have hitherto been regarded as the male sexual organs, are the anthers. The pollen grains contained within the anthers enclose a semi-fluid matter, the fovilla, composed in great part of minute globules, the nature of whose motions is yet a subject of disputation.†

The pistil is usually regarded as the female part of the flower; its upper part is called the stigma; and its lower part is the ovarium, or germen, in which the ovula are formed long before impregnation. The stigma and ovarium are united by the style. The style is formed internally of cellular tissue, which either occupies the whole thickness of the style as low as the ovarium, or more commonly includes a central cavity, which extends from the stigma to the ovarium, where it divides into as many branches as there are ova. The ovulum has generally two coats, or integuments, the primine and secundine, which enclose the cellular nucleus or perisperm. (See fig. 164.) Both coats of the ovulum are connected with the ovarium through the medium of the funiculus which transmits the vessels that terminate in the primine and secundine. Both these coats also present at another point an opening, the micropyle or foramen, which leads to the internal portion of the ovulum, or the nucleus. In many plants the nucleus projects through the foramen in the form of a conical prominence. In the interior of the nucleus is a cavity, the sac of the embryo, which is formed by a single cell, and is of great importance in the process of fecundation. (See fig. 165.)

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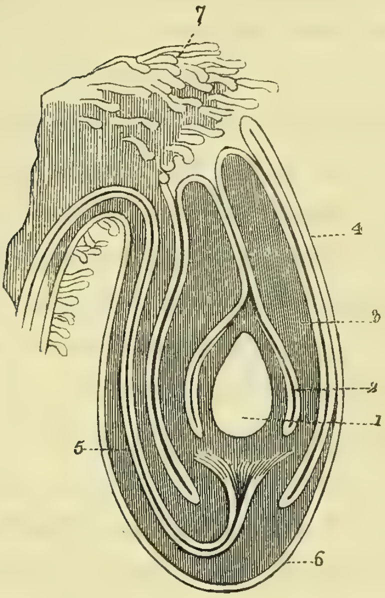
* [See the account of Dr. Barry's observations on the process of fecundation in Mammalia at the end of the present chapter.]

† See Meyen, op. cit.

Fig. 164.[*]



At the period of fecundation the anthers of hermaphrodite flowers approach the stigma, and shed their pollen upon it. In plants of which the sexes are distinct the pollen is conveyed to the female ovaria, often from a considerable distance, either by the wind or by insects. The intimate steps of the process of fecundation have been brought to light by modern researches. Amici observed that the pollen grains, when received upon the stigma, emitted tubes. Brogniart traced these elongating tubes into the tissue of the stigma. They are productions of the inner coat of the pollen grain, and increase in length by true vegetative growth, and by the appropriation of nutritive matters which they derive from the stigma. More recently the pollen tubes have been found to extend through the canal of the style, or its cellular tissue to the ovulum, and have been ascertained to enter the foramen or micropyle. The nature of the act of fecundation has thus, by the observations of Robert Brown, Horkel, Schleiden, and Meyen, been fully established in the case of many plants. These observations, however, have led to differences of opinion respecting the sexes of plants. Mirbel regarded the act of fecundation as the engrafting of a male cell upon a female cell. According to Schleiden's observations,[†] on the contrary, the pollen tube itself becomes the future embryo. He describes the extremity of the pollen tube as entering the foramen of the ovulum, as pushing the embryo sac before it, and as becoming imbedded in it. (See fig. 165, A.) The part thus included in the ovulum, according to Schleiden, becomes separated by a constriction, and detached from the rest of the pollen tube; forms the rudiment of the future embryo; and is the nidus for the development of new cells. (See fig. 165, B.) According to this description, which is based on numerous observations, the doctrine of the sexes of plants must be entirely reformed, and the parts hitherto regarded as the female sexual organs must be viewed merely as a kind of uterus, in which the embryo is nourished. Other writers, and especially Treviranus and Meyen, support the old theory of the sexuality of plants.

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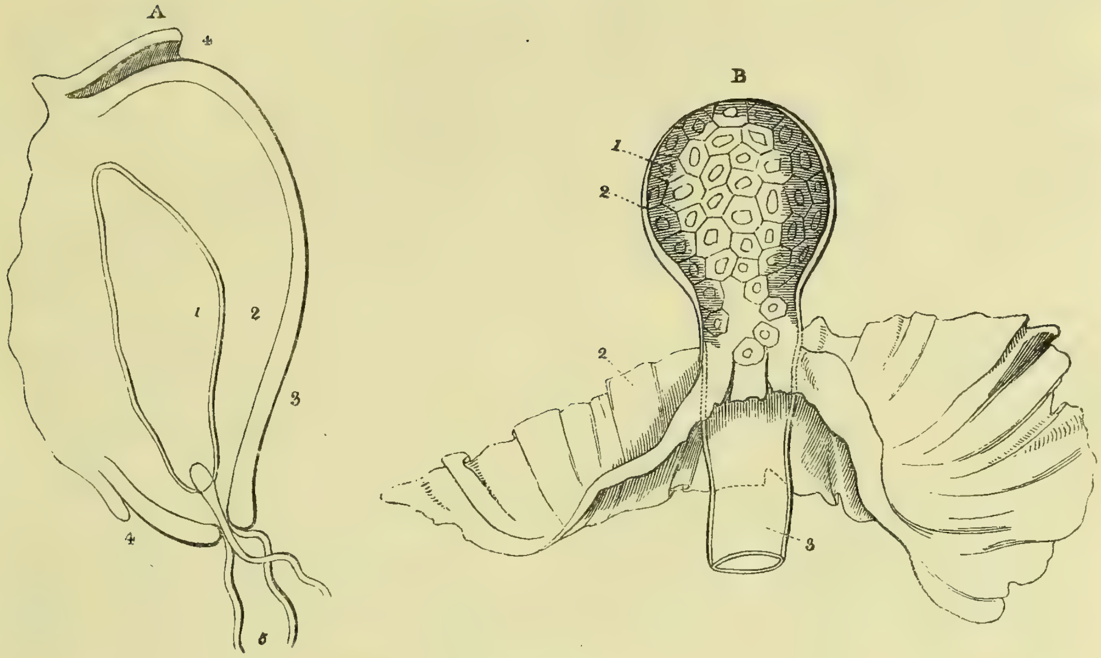
[*] [Ovulum of Linum pallescens. After Schleiden, Nov. Act. Nat. Cur. t. xix. 1. embryosac; 2. nucleus; 3. secundine; 4. primine; 5. raphe; 6. cuticle; 7. placenta.]

[†] Wiegman's Archiv. 1837, t. i. p. 291. Nov. Act. Nat. Cur. t. xix p. 1.

Fig. 165.*



According to Meyen the pollen merely introduces into the cavity of the nucleus a small quantity of fecundating substance, which unites with the organizable mass of mucus or gum contained in the embryosac. The part of the pollen tube which has coalesced with the cavity of the nucleus, or with the embryosac, being nourished by the organic mucus of that cavity, or of the embryosac, assumes the form of a sac or vesicle, in the interior of which cells are developed. But the pollen tube itself is at the same time detached. The vesicle which is formed in the cavity of the embryosac after the pollen tube has entered it, or which, in other words, is formed after the union of the pollen tube and embryosac, is called by Meyen the germinal vesicle. The embryo is produced by the vegetation of this vesicle, or by the formation of cells in its interior.

In considering the nature of the process of fecundation in plants, observation and theory must be entirely separated. The question to be decided therefore is, whether the extremity of the pollen tube does penetrate the nucleus of the ovulum, pushing the embryosac before it, and then being separated from the rest of the tube, actually becomes the embryo itself? or, whether, as Meyen maintains, the part called by him the germinal vesicle, is a new structure, produced by the union of the fecundating contents of the pollen tube and the mucous matter of the embryosac.*

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* [Fig. 165. A. Ovulum of Secale cereale, at period of fecundation, divided longitudinally; 1. embryosac; 2. nucleus; 3. secundine; 4. primine divided; 5. pollen tubes, one of which has entered the nucleus, and forms the commencement of the embryo in the embryosac. Fig. 165. B. Apex of the embryosac of Phormium tenax, inverted by the end of the pollen tube, which is already filled with delicate nucleated cells, constituting the embryo. 1. the end of the pollen tube in the inverted portion of 2, the embryosac; 3, the pollen tube. After Schleiden. Nov. Act. t. xix.]

The development of intermediate forms in hybrid generation proves that both the male and the female plant contribute equally to determine the organisation of the new individual; but does not decide the question in favour of either of the two above-mentioned views respecting the nature of the fecundating process and the sexes of plants. For even if, as Schleiden supposes, the embryo is merely a portion of the pollen tube inserted into the nucleus of the ovulum; if this portion of the pollen tube, therefore, is *in form* the embryo; still it may be greatly influenced and modified in its endowments by forces resident in the fluids of the nucleus; and if such be really the process, it will merely prove fecundation to consist in a part of the pollen tube being rendered capable of vegetation in the peculiar form of the species by being subjected to the action of the nucleus. The pollen tube is capable of vegetative growth, independently of this influence, and begins to manifest that power before reaching the nucleus; but it is not capable of developing the entire organisation of the species. In animals the part which, by fecundation, is made capable of vegetation, namely, the germ, is derived from one of the sexes, and the unimpregnated germ does not perceptibly differ in form from the germ which is impregnated.

It remains for future observations to determine whether the pollen grain, or the part hitherto called the ovulum of plants, corresponds to the germ produced by the female animal.

[Dr. Barry† has made some remarkable observations relative to the changes which take place in the ovum immediately after impregnation, — observations which seem to bring us much nearer to a perfect acquaintance with that process. In immature ova, according to

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* [Meyen has recently published some further remarks on the acts of impregnation in plants (Noch einige Worte über den Befruchtungs-akt und die Polyembryonie, von F. J. F. Meyen, Berlin, 1840). He still denies the correctness of Schleiden's observations. The essential part of the process of impregnation consists, he says (p. 11), of the complete coalescence of the end of the pollen tube with the wall of the embryosac, which he compares to the conjugation of conferva (see fig. 167, p. 1505). The germinal vesicle is formed from the substance of the united membranes, namely, from the extremity of the pollen tube and the apex of the embryosac also. There is at first a free communication at the point of coalescence between the cavities of the pollen tube and embryosac. The substances contained in them, therefore, become mixed. During the development of the germinal vesicle these substances afford nutriment to it, and when its cavity has become separated by septa from the pollen tube and the embryosac, they form within the vesicle the primary mass from which the embryo is developed. Valentin (Repertor, 1840, p. 61) objects to the application here made of the term germinal vesicle; since, according to analogy with the generative process in animals, the germinal vesicle should be a part which exists before impregnation.]

† Researches in Embryology, second series, Philos. Transact. 1839, pt. ii. pp. 312 to 316.

Dr. Barry, the germinal vesicle is situated at the centre of the yolk; but subsequently it passes to the surface. The ovum itself lies at first in the centre of the Graafian vesicle; but previously to impregnation is conveyed to that part of its surface which is nearest to the exterior of the ovary, and is held there by the "retinacula," described at page 1470. The germinal spot is at the same period placed at the surface of the germinal vesicle. Such is the condition of the mature ovum, *ante coitum;* that is to say, its essential parts lie as near as possible to the surface of the ovum and Graafian vesicle. *Post coitum,* but before the discharge of the ovum from the ovary, the germinal spot passes to the centre of the germinal vesicle, and the germinal vesicle to the centre of the yolk. The nature of these changes in the condition of the ovum, taking place after coitus, and the fact of spermatic animalcules having been traced to the ovary itself, render it exceedingly probable that these changes are produced by the contact of the seminal fluid. In further, and more minute researches,* directed to discover the state of the ovum at the moment of fecundation, as well as immediately before and after that event, Dr. Barry has made the following important observations:—He finds that the germinal vesicle is really the essential portion of the ovum, and that it is the seat of the most important changes which immediately follow impregnation. "It is known that the germinal spot presents, in some instances, a dark point in its centre. The author finds that such a point is invariably present at a certain period; that it enlarges, and is then found to contain a cavity filled with fluid, which is exceedingly pellucid. The outer portion of the spot resolves itself into cells; and the foundations of other cells come into view in its interior, arranged in layers around the central cavity; the outer layers being pushed forth by the continual origin of new cells in the interior. (See fig. 166, A. B. C.) The latter commence as dark globules in the pellucid fluid of the central cavity." "The germinal vesicle, enlarged and flattened, becomes filled with the objects arising from the changes in its spot, (see fig. 166, C;) and the interior of each of the objects filling it, into which the eye can penetrate, presents a repetition of the process above described. The central portion of the altered spot, with its pellucid cavity, remains at that part of the germinal vesicle which is directed towards the surface of the ovum, and towards the surface of the ovary. *At the corresponding part, the thick transparent membrane of the ovum, in some instances, appears to have become attenuated, in others also cleft.* (Fig. 166, D.) Subsequently the central portion of the altered spot passes to the centre of the germinal vesicle; the germinal vesicle, regaining its spherical form, returns to the centre of

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* [Researches in Embryology, third series, read at the Royal Society, May 7, 1840; see London and Edinb. Phil. Mag. June, 1840, and Phil. Transact. 1840, pt. ii. p. 529.]

Fig. 166.*

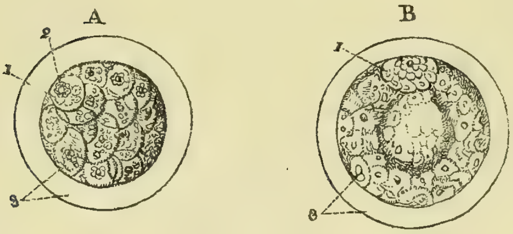


Fig. 166.*

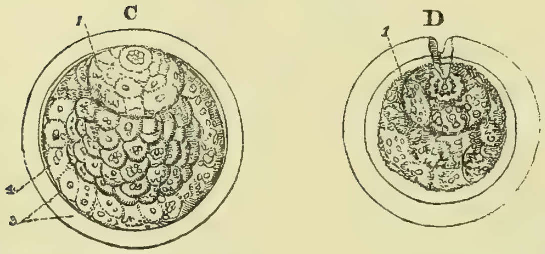
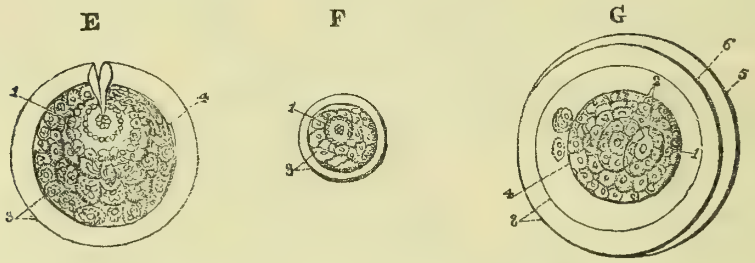


Fig. 166.*



the ovum, and a fissure in the thick transparent membrane is no longer seen. (Fig. 166, E. F.) From these successive changes it may be inferred that fecundation has taken place; and this by the introduction of some substance into the germinal vesicle from the exterior of the ovary. It may also be inferred, that the central portion of the altered germinal spot is the point of fecundation. In further proof that such really is the case, there arise at this part two cells, which consitute the foundation of the new being. These two cells enlarge, and imbibe the fluid of those around them, which are, at first, pushed further out by the two central cells, and subsequently disappear by liquefaction. The contents of the germinal vesicle thus enter into the formation of the two cells. (Fig. 166, G.) The membrane of the germinal vesicle then disappears by liquefaction." The further changes which the two cells here referred to undergo, preparatory to the formation of the embryo, will be detailed at a subsequent page. It remains here only to state that the observations above related were made on the ovum of the rabbit; but that Dr. Barry has found the corresponding parts in the ovum of birds, batrachia, and osseous fishes, to be the seat of the same changes. He believes the whole substance of the cicatricula in the laid egg of the bird to have its origin within the germinal vesicle, and not to be merely the discus vitellinus, or proligerus of the unfecundated ovum in an altered state.] [For further observations on the process of fecundation, see the Appendix.]

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* [Fig. 166 represents the changes which, according to Dr. Barry, take place in the ovum of the Rabbit at the time of impregnation and immediately subsequent to it. A. is an ovarian ovum taken from an animal killed seven hours post coitum. The Graafian

CHAPTER VI.

THE THEORY OF SEXUAL GENERATION.

a. Casper Fried. Wolff's theory of the fecundation of plants and animals.[*]

THE fundamental notion on which Wolff bases his theory of conception is, that in fructification the vegetation of plants attains its end, and that as soon as flowers are developed at the extremity of the axis of a plant, that part becomes incapable of prolonging the axis by the formation of leaf buds. He then shows that the organs of fructification are merely modified leaves. The calyx of the sunflower, he says, is composed of a number of leaves smaller than the ordinary leaves of the plant, closely aggregated together. The petals, again, are merely leaves, as is evident in the grasses. The corolla of grasses is not distinguished from the calyx (or paleæ), and differs from the ordinary large leaves of the grass in no other respect than the calyx differs from them. The colour of flowers is not essential and often is gradually developed. The flower of Statice has many calyces, of which the most inferior is pale and devoid of colour, the next succeeding more and

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vesicle exhibited no appearance of preparation for discharging its ovum; 1. the germinal vesicle is spherical; 2, the germinal spot exhibits incipient cells at its margin. The layer of substance immediately within the thick transparent membrane, or zona pellucida, 3, is composed of regular elliptical flattened cells. B. is an ovarian ovum, more nearly prepared for fecundation. The germinal vesicle, 1, is enlarged and flattened, and is filled with the cells developed from the germinal spot. The flattened cells on the inner surface of the zona pellucida, 3, are indistinct from partial liquefaction. C. an ovum from a Graafian vesicle which was large and vascular. The germinal vesicle, 1, is larger, and the cells within have increased in number. Between the outer layer of cells of the yolk and the zona pellucida, 3, a distinct membrane is seen. This was described by Dr. Barry, in the second series of his remarks, as the proper membrana vitelli; but he now states that it has no permanent existence, but is formed as each layer of cells approaches the zona pellucida, and disappears when those cells undergo liquefaction. D. In this ovum the pellucid centre of the altered germinal spot lies immediately under an orifice or cleft in the thick transparent membrane. An object resembling a Spermatozoa was observed by Dr. Barry in this orifice. 1, indicates the outline of the germinal vesicle. E. Here the cleft in the thick transparent membrane, 3, is still visible; but the germinal vesicle, 1, filled with cells, is returning to the centre of the ovum. The membrane, 4, separating the yolk cells from the thick zona pellucida, is again formed. F. shows the germinal vesicle, 1, nearly in the centre of the ovarian ovum and the germinal spot or point of fecundation in the centre of the vesicle. G. is an ovum from the Fallopian tube. The germinal vesicle, 1, of which the outline can be scarcely distinguished, contains two cells, 2, much larger than the rest; the cells of the yolk mass are surrounded by a proper membrane, 4, between which and the zona pellucida, 3, is a fluid. Two minute cells have escaped liquefaction in this fluid. The incipient chorion, 5, is beginning to imbibe fluid, 6, and to rise from the zona pellucida.]

[*] Theorie der Generation. Halle, 1764, p. 222.

more inclined to red, and the most superior, like the flower itself, of the deepest red, although its figure is not different from that of the other calyces. The seed-vessels are evidently modified leaves, for, when they are ripe and dehisce, each valve appears as a true leaf. The same is the case with the seeds. As soon as they are put into the ground, their lateral halves, or cotyledons, become transformed into leaves.

Wolff next demonstrates that the modification which leaves undergo in the formation of the flowers is dependent on an arrest of the vegetative process. The leaves which constitute the calyx of the sunflower are, he observes, scarcely one-eighth part so broad as the ordinary leaves of the plant, and are much shorter. The leaves forming the calyx (or bracts) and flower of the grasses are scarcely one-fifth part so long as the perfect leaves. He adds, that the proper leaves of a plant gradually become imperfect as they are nearer to the organs of fructification, and remarks that this is so much the case in the sunflower and many other plants, that it is impossible to say where the ordinary leaves cease and those of the calyx begin. It may be added, that the internodia of the stem are shorter and shorter in proportion as they are nearer to the flowers, and that in the position of the sepals composing the calyx of many plants, the spiral arrangement of the leaves of the stem can still be distinctly traced. The vegetative action, therefore, says Wolff, evidently becomes more imperfect and weaker towards the point of fructification; and it must, at length, entirely cease. This perfect arrest of vegetation takes place in the seeds. The want of nutritive juices is the cause of the arrest of vegetation, as is shown by the withering and fall of the fruit. If a plant which is known to put forth leaves a certain number of times, for instance, six times, before developing the organs of fructification, is set in a very poor soil, not only will its leaves generally become very small and imperfect, but it will scarcely have put forth leaves three times before fructification will take place. If this same plant is placed, not in poor, but in a very moist and rich soil, its leaves will become larger and more perfectly formed, and instead of developing leaves six times, it will put them forth nine times before it shows the organs of fructification. Moreover, if, while the fructification of a plant is thus delayed by the richness of the soil, it is transplanted to a poor soil, flowers will immediately appear. Lastly, if a plant which has already developed the calyx and rudiments of the corolla and anthers in poor soil, is quickly transplanted to rich soil, the anthers can be seen to become transformed into petals in consequence of the excess of nutriment.

In the next place, Wolff remarks that the first parts of the young plant, developed by the power of the male semen, do not differ from the ordinary leaves of the parent plant. The young plumula, is, like the leaf-bud of the parent plant, composed of young leaves. Both, therefore, require for their development the same agency or cause, which was in operation in the old plant when it produced its ordinary leaves. The male semen, or the pollen, must be this cause of vegetation, which was previously deficient; or, in other words, it must be nutriment in its highest perfection. The afflux of the ordinary nutriment of the plant to the extremity of its axis by the ordinary passages, ceases; but the male semen, or pollen, is a kind of nutriment, which, instead of being conveyed through the ordinary channels, is supplied from without to the parts of the plant destined to undergo vegetation.

Wolff explains the phenomenon of conception in animals in the same way. The ovary is the part of the animal organism in which the vegetative action is arrested, and hence it may be compared to the imperfectly developed terminal bud of plants.

b. Critical examination of Wolff's theory.

In Wolff's theory of conception there is much that is perfectly correct, but its main conclusion is erroneous, and involves a false view of the nature of semen. It is quite true that fructification is the result of abortive vegetation; but this abortive development is of an extraordinary kind, and cannot be removed by the most perfect nutriment A deciduous leaf-bud is also abortive in its vegetation, and was so, even before its separation from the parent plant; there are leaf-buds, as we have seen, which consist merely of a single cell, and which, therefore, are quite as simple as the germ formed in fructification; and, nevertheless, these leaf-buds in their internal condition and endowments are totally different from the germs of the organs of fructification. All that the deciduous bud requires for its perfect development is, that new nutriment should be supplied to it from without, either by the soil or by another vegetating organism, on which it is engrafted. The semen of the male, on the contrary, far from merely yielding nutriment, however perfect, to the unimpregnated germ, really contains within itself, just as the germ of the female does, the power of determining the whole form of the species, whether plant or animal. This fact is evident in ordinary generation, as well as in the production of hybrids. The offspring in ordinary generation, possesses, not merely the properties of the mother, but those of the father also in an equally marked degree. This is matter of constant observation, in the generation both of man and of animals. The race, form of body, propensities, passions and talents of the father, as well as of the mother, are manifested in the progeny; and since these peculiarities are communicated to the germ by the semen, they must be contained in it, just as those of the female parent are contained in the germ. The same evidence is afforded by the intermediate forms resulting from the intermixture of different species. The mule partakes of the characters of both the horse and the ass; and the hybridising of plants as frequently gives rise to intermediate forms distinct from either parent plant, and not to be regarded as merely aborted individuals of either species. Hence, if the semen be denominated nutriment, it must be regarded as a kind of nutriment in which, no less than in the germ, are involved the specific form of the animal or vegetable, and all its individual peculiarities.

In the same way we may refute the theory of those physiologists, who regard the semen not as nutriment, but, on the contrary, as an agent which arrests the vegetation of the germ and the growth of the axis of the plant. For this arrest of vegetation occurs in plants where there are merely female flowers, and where no influence of the fecundating principle could be exerted. Moreover, since this fecundating principle has the power of determining the form of the male individual, it can be neither a mere stimulus nor an agent which simply arrests vegetation.

c. *Of the nature of the ovum and semen, and of the process of conception.*

The unimpregnated vegetable germ and the leaf-bud agree in both possessing "potentially" the specific form of the plant. They differ, however, from each other, in the flower-bud which contains the unimpregnated germ being unable, of itself, to put forth new buds; while the leaf-bud not only can develop itself to a new individual, but may become the stock from which an infinite number of new individuals are developed. The unimpregnated germ, therefore, though involving "in potentiâ" the form of the species, yet is, in consequence of a peculiar impediment to its organising action, unable to develop this form "in actu"; but the leaf-bud is free from such impediment. The organising action of a leaf-bud is certainly impeded when the nutriment necessary for vegetation is not supplied to it, as may happen to a deciduous leaf-bud. But the impediment to the organisation of the unimpregnated germ is much more intimately connected with its own constitution; for the germ does not undergo development even when it is supplied with the necessary nutriment. What, then, is the nature of this cause which prevents the organising action of the germ from being exerted? Since it is not merely want of nutriment, it most probably consists in the germ having defects in its constitution from which the leaf-bud is free, and which render the development of the germ in the pre-ordained form impossible. The semen or fecundating matter contains that which gives integrity to the germ. The semen, also, is capable of determining the specific and individual form of the new animal or plant, but it likewise is the subject of a defect which renders it incapable of actually developing that form, until it has united with the female germ. The defects, however, of the ovum, or germ, and of the semen, are not identical in their nature, since each contains that in which the other is deficient. The ovum and semen are not similar halves of one whole. The ovum, at least that of animals, contains the part destined to germinate, and is, in fact, the primary cell, or contains the primary cells, which form the basis of the new organism, and maintain, unbroken, the chain of organisation. The semen, on the contrary, does not itself germinate, but is a fluid excitor of germination, endowed, at the same time, with the power of determining the form not only of the species but of the individual organism which produced it.

It may here be well to glance at the mode of vegetation of cells within developed organisms. The cells of vegetables have the power of transforming the nutriment brought into contact with them into a fluid productive matter, within which new cells are developed. The formation of the new cells in this plastic matter, the "cytoblastema" of Schleiden, is determined by the influence of a pre-existing cell, and is effected by a definite process; nuclei being first formed, around which the young cells are developed. Schwann's researches have shown that the cells of the animal organism grow in the same way. The germ, therefore, which is really a cell, may be regarded as a primary cell endowed with the power of producing the specific form of the plant, but defective in the respect of being incapable of producing the "cytoblastema." The semen or fecundating matter, on the contrary, though capable of determining the power of the new organic being, contains no primary cells, but resembles, more nearly, a "cytoblastema," endowed with the property of producing a definite form, but incapable of vegetating except under the influence of a primary cell already formed. We may imagine, that when the primary cell of the germ, and the "cytoblastema" of the semen are brought together, the vegetation of the primary cell will commence; while, in consequence of both the primary cell of the germ and the plastic matter of the semen exerting an influence on the products of this vegetation, the new individual must present a mixture of the forms which the germ and semen had respectively a tendency to give, and will resemble both the male and the female parent.

Conception is not the only instance in which two organisms, both of which have the power of assuming a definite form, exert a reciprocal influence on each other; nor does it, indeed, afford the only example of the complete union of two substances endowed potentially with specific forms, so as to produce one individual. In order to perceive more clearly the peculiar nature of the process, it will be useful to consider for a moment that kind of organic union, in which two distinct forms do not become fused into an intermediate one. The extreme cases which present themselves in the union of two organisms are found, on the one hand, in the engrafting of a leaf-bud upon a different stock, and, on the other hand, in the mingling of the forms of the parents, which takes place in sexual generation. Another phenomenon similar to the latter of these two extremes, is the coalescence of two buds or gemmæ, such as takes place in the process of conjugation.

1. *Engrafting of buds.* The majority of facts tend to prove, that cuttings or buds grafted upon a new stock undergo no modification from the influence of the stock on which they grow, nor themselves produce any modification of its vegetation. The evergreen oak engrafted upon the common oak, the leaves of which fall in the winter, keeps its leaves during that season. The laurel engrafted upon a wild cherry-tree, remains in leaf through the winter, while the cherry-stock becomes stripped of its leaves in the autumn.* Poor sorts of pears engrafted on pear-trees of a good kind, yield poor fruit, and vice versâ. In the cases where the white jasmin, on which yellow jasmin had been engrafted, is said to have borne yellow flowers on those branches which issued from the trunk below the situation of the graft; the flowers thus apparently modified did not, according to Meyen, belong to the stock, but to the graftling which had developed adventitious buds from layers of its wood sent down between the bark and wood of the stock. It appears, therefore, that the changes which graftlings undergo, are, for the most part, limited to the improvement of the fruit, and to those modifications which may also be produced by the change of soil and of the nutriment thence derived. Grafting, either of cuttings or of leaf-buds, is, indeed, a means of preserving pure and unchanged the forms of species and even of varieties, which it is much less easy to do by sexual propagation, since, in the latter process, the form is determined equally by two different influences. The slight influence exerted on each other by two organisms which have coalesced is evinced in animals as well as in plants; it is a well-known fact, that double monsters, when they live sufficiently long, as in the case of Rita and Christina, may manifest different dispositions of mind and temper.

2. *Conjugation or coalescence of two buds.* Although perfectly developed and organised individuals which are organically united, cannot modify each other's form and endowments, yet it might be conceived that two buds or gemmæ, would not merely exert a modifying influence on each other, but would even become fused into one organism. This idea is suggested by the experiments which have been instituted on the Hydra. Each fragment of a Hydra, isolated from the body of the animal may be regarded as a bud. The posterior or lower part of a polype separated from the rest of the animal is developed into an entire new individual, but if this posterior part when thus separated is again applied to the anterior portion, and their cut surfaces be kept in apposition, union

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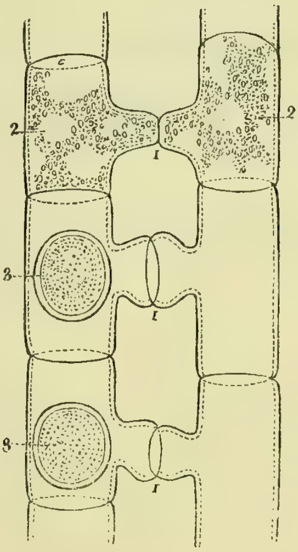
* Meyen, Pflanzen-physiologie, t. iii. p. 92.

takes place, and the part which had been isolated from it becomes again subject to the centre of individual life resident in the anterior part of the animal.

This experiment, related by Trembley, leads us to imagine further, that even two portions of a Hydra, neither of which as yet contains a ruling centre of individual animal life, but which, nevertheless, are capable of becoming new individuals, might, if they were brought into sufficiently close contact, coalesce, and form a single bud from which a single individual would be developed. Amongst the various experiments instituted by Trembley, this also occurs. In no instance, however, did it succeed; the two fragments did not unite, and there was, consequently, no fusion of two portions of organic substance, comparable to that which takes place in sexual generation. The two fragments of the polype were capable of assuming the properties of buds, but as yet they had not undergone this change. In some of the lowest organic bodies, however, there are instances of the actual fusion of two buds into one.

Fig. 167.†



The process of conjugation was first observed by O. Fr. Müller in the Confervæ; it is presented by the Confervæ conjugatæ, and especially by the genera Conjugata and Spirogyra. Ehrenberg* observed the phenomenon in a fungus (Syzygites); and it was witnessed by the same physiologist and by Morren in the Closteria. At the time when conjugation is about to take place, bud-like processes or excrescences appear on the segments of the Confervæ: the processes belonging to contiguous filaments unite, and their walls becoming absorbed, the conjugate segments communicate freely with each other. (See fig. 167 at 1.) The mucous mass (2) contained in the segments or cells, moulds itself into the form of a ball and passes from one cell into the other where the masses of the two cells unite and form a spherical body, the spore (3). In each of the conjugate filaments some cells are the recipients, while others yield their contents to the opposite cell of the contiguous filament. Vaucher observed, that in some cases, the contents of the two conjugate Con-

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[*] Verhandl. der Gesellschaft naturforsch. Freunde zu Berlin, B. i. 1829.

[†] [Conferva bipunctata (Stellulina cruciata, Link) in the act of conjugation. 1, The bud-like processes of the cells uniting; those of the two lower cells of the filaments have coalesced, and their cavities communicate freely. 2, Contents of the cells before conjugation is completed. 3, The spores resulting from the process. After Meyen, Pflanzen-physiologie, t. iii. taf. x. fig. xi.]

fervæ united in the intermediate tube.* The two masses which unite to form the globular spore in the conjugation of Confervæ must be regarded as of the nature of buds and not as two different substances analogous to germ and semen, for, in the first place, their external characters are identical, and secondly, spores, or rather buds, exactly similar to those produced by conjugation, are likewise found in segments of Confervæ, quite independently of conjugation, for example, in the Spirogyra, according to Meyen.

3. *Coalescence or fusion of the germ and semen in sexual generation.* Conjugation is apparently a simple fusion of two perfectly similar gemmæ or buds. This is evidently a higher form of generation than propagation by the formation of simple buds. For the bud resulting from the process of conjugation, must participate in the individual peculiarities of two individuals, while the simple bud has the endowments of one only. This seems to be the principal purpose, also, of the sexual mode of generation, namely, the production of an offspring with the endowments of the whole family and species, and not merely with those of a single individual. Sexual generation differs, however, from conjugation, in the circumstances of the productive matter of the one sex being the necessary complement of that of the other sex; of the one being always the recipient and the other always the additament; and of the one having already an organised form, while the other is still fluid with merely a tendency to become organised.

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* For an account of the conjugation of the Closteria, consult Morren, Ann. des Sc. Nat. t. v. 1836, p. 257; and Ehrenberg, die Infusions-thierchen, Tab. v. vi.

BOOK THE EIGHTH.

Of Development.

SECTION I.

Of the development of the ovum and embryo.

THE development of the embryo of vertebrate animals is presented to us in its most simple form in fishes and the amphibia. Hence it is most convenient to study the process in these classes before proceeding to consider its details in the higher Vertebrata. The ovum of fishes and Amphibia has neither the amnion nor the allantois,—parts which are common to the ova of birds, reptiles, and Mammalia. Aristotle first discovered that fishes, though furnished with the yolk sac in their embryonic condition, have not the allantois. "The ova of fishes," he says, "have not the umbilical duct which passes to the chorion under the shell in birds, although they have the umbilical duct which leads to the yolk."* All the phenomena of development in these lower Vertebrata consist, therefore, of the changes which the germinal membrane, the embryo produced from it, and the yolk sac undergo. The formation of the embryo and yolk sac conforms in all the Vertebrata to one common type. This type suffers modifications in the different classes; and like the whole process of development, it is comparatively simplified in fishes, and still more so in Amphibia. In the latter class the entire germinal membrane, and the part analogous to the yolk sac of other animals, is expended in the formation of the embryo, while even in many fishes a yolk sac exists distinct from the part which forms the embryo.†

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* *Πρῶτον μὲν γὰρ οὐκ ἔχουσι τὸν ἕτερον ὀμφάλον τὸν επὶ τὸ χόριον τείνοντα ὃ ἐστιν ὑπὸ τὸ περιέχον ὄστρακον.*—Aristotle, De generatione animalium, iii. 3.

† The principal works which treat of development generally in all the classes of animals, are those of Dutrochet, Récherches sur les enveloppes du fœtus, in Mém. de la Société Méd. d'Emulation, t. viii. and his Mém. p. s. à l'hist. anat. et physiol. des Végétaux et des Animaux. Paris, 1837, t. ii. p. 200; Burdach, Physiologie, Bd. ii. 2te Aufl. mit Beiträgen von E. Von Baer, Rathke, Meyer, Von Siebold und Valentin. Leipzic, 1837; Von Baer, Entwickelungsgeschichte der Thiere, i. Königsb. 1828, ii. 1837; Valentin, Entwickelungsgeschichte, Berlin, 1835; and R. Wagner, Physiologie, i. Leipz. 1839.

CHAPTER I.

DEVELOPMENT OF FISHES AND AMPHIBIA.

1. *Changes which take place in the yolk, previously to the formation of the embryo.*

In all animals some changes in the entire mass of the yolk seem to precede even the first modelling of the embryo. The extent of these changes, however, is very different in the different classes. They are least considerable in birds, and most so in Amphibia, fishes, and many invertebrate animals: in which they produce the phenomenon of the regular division and subdivision of the whole yolk.

The phenomenon of the division and subdivision of the yolk was first discovered in the ova of frogs, by Prevost and Dumas.* Further valuable observations on the subject have since been made by Rosconi,† Baumgaertner,‡ and Von Baer.§

The surface of the yolk of the frog's ovum presents a well-known difference of colour in its two halves; the one half being black, owing to the presence of a thin layer of black matter at that part, and the other being of a lighter colour. In the middle of the dark area there is a point where the black stratum is interrupted, and from this point a canal leads to a cavity somewhat deeper seated in the mass of yolk. A line passing from this middle point of the dark surface of the yolk to the middle of the lighter-coloured surface, is called by Von Baer the axis of the ovum. Furrows extending over the surface of the yolk from the one point to the other are called meridian-furrows; those which run in a plane perpendicular to the axis are equatorial furrows or parallel furrows, according to their distance from the middle points of the two areæ.

The following is Von Baer's description of the process of division and subdivision, or furrowing of the yolk. At the end of the fifth hour after the expulsion of the ovum from the female frog, the first meridian-furrow is formed; beginning at the middle of the dark surface. (Fig. 168, A. I.) This is not a mere superficial furrow, but is a cleft extending through the whole mass of yolk, so as to divide it into two contiguous ellipsoid masses. Before this complete division of the yolk into two hemispheres has taken place, and about six or seven hours after impregnation, the second meridian-furrow appears. This crosses the

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* Ann. des Sc. Nat. t. ii. 110.

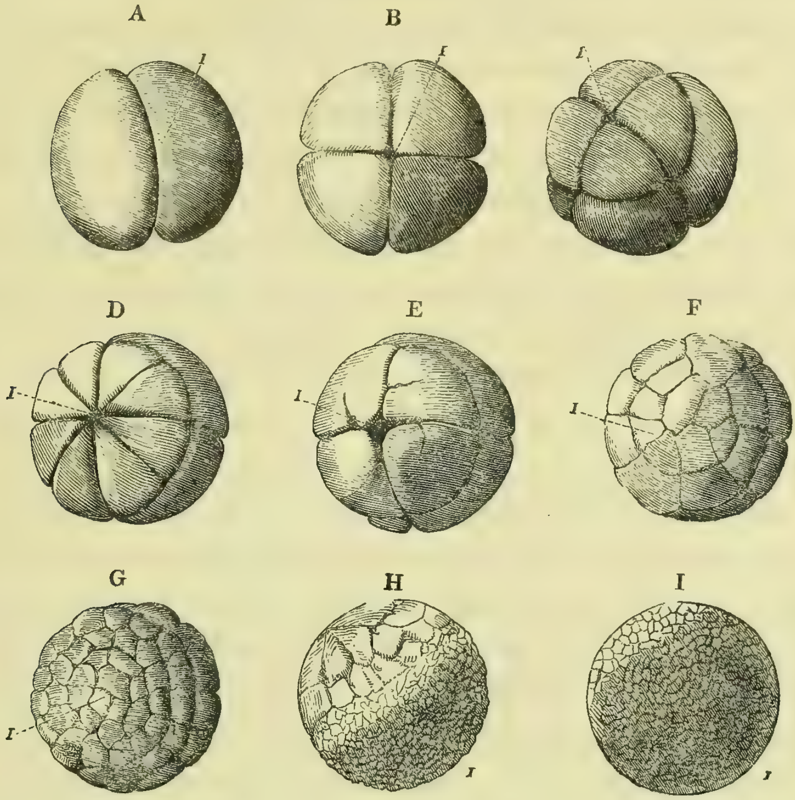
† Développement de la grenouille commune. Milan, 1826.

‡ Ueber Nerven und Blut. Freiburg, 1830.

§ Müller's Archiv. 1834, 481.

first at right angles. (Fig. 168, B.) An ovum in this state, which has been frozen, consequently splits into four segments of a sphere. The equatorial furrow soon makes its appearance. (Fig. 168, C.) Then new meridian furrows, and in a short time parallel furrows show themselves, until the yolk acquires the form of a blackberry or raspberry. (Fig. 168, D—G.) Lastly, the surface of the yolk becomes again perfectly smooth. (Fig. 168, H. I.) This cycle of changes may be passed through in the course of twenty-four hours. Soon afterwards the formation of the embryo commences. The lighter-coloured portion of the surface, according to Von Baer, becomes smaller and smaller, in comparison with the darker portion, and at the same time acquires an elongated form. It then becomes marked off at one end from the darker surface by a black line. This black arched line forms at length a slight depression, and the posterior extremity of the embryo is thus defined. Its anterior boundary is not so soon visible, perhaps on account of its lying entirely within the dark portion of the surface of the yolk.†

Fig. 168.*



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* [Fig. 168. The yolk of the frog's ovum undergoing the process of division and subdivision. The cypher 1 in all the figures indicates the centre of the dark surface of the ovum. After Von Baer. Müller's Archiv. 1834.]

† [Some microscopic observations by M. Bergmann of Gottingen on the structure of the smaller masses into which the yolk of the batrachian Amphibia becomes subdivided are contained in the first number of Müller's Archiv. for 1841. He finds that each of these masses is surrounded by a distinct membrane, and contains in its centre a solid transparent corpuscule.]

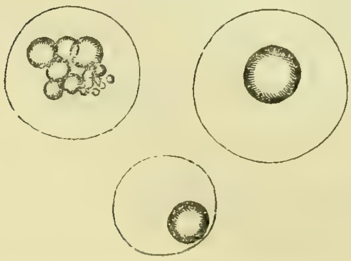
The division and subdivision of the yolk in the ova of fishes have been described by Rusconi.* Having impregnated some ova of the tench artificially, he observed that they soon afterwards lost their spherical form, and became pear-shaped, owing to the formation of a kind of intumescence at one part of the surface of the ovum. The small granules previously dispersed through the yolk now became collected at the base of this intumescence. Half an hour after the occurrence of this first change, two furrows, intersecting each other at right angles, appeared at the prominent part of the yolk. A quarter of an hour later two other furrows were observed at each side of the first, so that the prominent part of the yolk, which previously was divided into four lobes, now appeared to be formed of eight lobes. After the lapse of another quarter of an hour each of these eight lobes were seen to be subdivided into four smaller lobes, by the formation of six fresh furrows intersecting each other at right angles. At the end of another half hour several new furrows appeared, which crossed those which already existed, and subdivided the lobes of the prominent part of the yolk still further, rendering them so small and numerous that it was now scarcely possible to count them. The process continued until the surface of this portion of the yolk regained the smoothness which it had before the first furrow appeared.†

This process of subdivision of the yolk observed by Von Baer and Rusconi in frogs, salamanders, and the family of Cyprini among fishes, has been discovered to occur in many invertebrate animals also; for example, in the Crustacea by Rathke; in the nematoid Entozoa by Siebold, and in the Mollusca by Sars.

2. *Vegetative process which the cells of the yolk present during the development of the ovum.*

The yolk was discovered by Schwann to consist of cells. These cells have different characters in different parts of the yolk. In the bird's egg, the cells of the yolk cavity and of the canal leading from it to the cicatricula, are nucleated. (Fig. 169.)

Fig. 169.‡



The cells composing the yolk differ also in form in different animals. In fishes and the Amphibia they are most commonly spherical. In sharks (Scyllium, Acanthias, Squatina,) and in the Myxinoid fishes they are, according to my observation, elliptical. In the rays (Raja), their form is for the most part flat and quadrangular, with rounded edges and corners. The sharks and rays may therefore be distinguished even by the form of the yolk-cells of their ova. [In the Mammalia, according to Dr. Barry, they are oval flattened disks. See page 1514.]

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* Bibl. Ital. I. xxix. and Müller's Archiv. 1836, p. 278.

† Rusconi, loc. cit. Müller's Archiv. 1836, p. 281.

‡ [Fig. 169. Cells from the yolk cavity of the hen's egg, after Schwann.]

The yolk has the most essential share in the development of the embryo. In some cases it is the portion of the yolk called the germinal membrane, which more especially contributes to the production of the new animal; in other cases, as in the frog, the entire mass of the yolk has this function. Rusconi was perfectly correct when he remarked that the embryo of the frog was formed from the whole yolk. The discoveries of Schleiden and Schwann respecting the growth of cells throw an unexpected light upon this subject.

Schwann has shown that the ovum of animals is a cell; that the membrane of the yolk sac represents the cell membrane, or wall of the cell; the germinal vesicle, the nucleus; and the yolk, the contents of the cell. He has further shown that the cells of the yolk are produced, in a manner conformable with the law regulating the development of all cells, within their parent cell, the ovum; and that the substance of the embryo itself is at first composed of cells. Schwann has likewise remarked that the yolk must be regarded not as mere nutritive matter, but in the light of a body having life; since the cells composing it take an essential part in the formation of the embryo. These cells effect a chemical change in their contents during the process of development, in consequence of which the yolk loses its coagulable property. Schwann, therefore, compares the yolk in respect of the share which it has in nutrition to the albumen of the embryo of plants. The proper albumen or white of the bird's egg entirely disappears during incubation, being absorbed as nutriment for the chick.

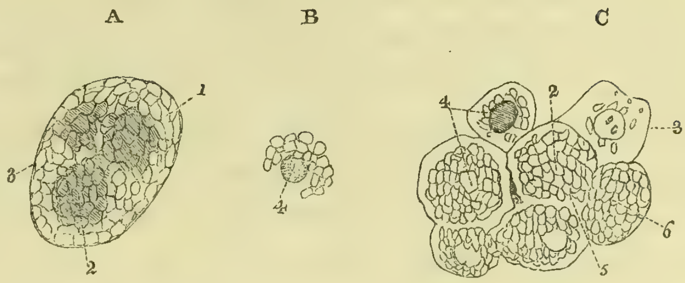
The further changes which the cells of the yolk undergo have been observed by Bischoff, Barry, and Reichert. Professor Bischoff and Dr. Barry recognised the development of cells within the yolk of the ovulum of Mammalia. Reichert has discovered that the formation of young cells within the previously existing cells composing the entire mass of the yolk is a process which continues during the whole period of development in frogs, where the entire yolk is employed in the building up of the embryo. In birds, according to the same observer, this process does not take place; the formation of young cells being there limited to that part of the yolk which more immediately contributes to the formation of the embryo.

In the ovum of the plagiostomatous fishes the cells of the yolk present transverse and oblique lines, resembling lines of division and subdivision, and frequently also constrictions corresponding to these lines. In the Squalus squatina the majority of the cells of the yolk have a line running in the longitudinal direction around each cell, and several transverse lines. In some cells oblique lines are seen, and in others which are irregular in form, these lines are also irregular, so as to divide the cells into several unequal segments. These yolk-cells of the ova of sharks and rays are contained in another cell, their matrix, which in the progress of development becomes filled with a fine granular matter. The appearance of the division and subdivision of the yolk-cells seems to be due to the circumstance of several cells lying in contact with each other. In some sharks the yolk-cells have a peculiar character. In the Scymni, for example, the granules of the yolk are large cells completely filled with numerous smaller cells which have been developed within them. In serpents and crocodiles, on the contrary, the remainder of the yolk, which is attached to the fœtus, contains many large cells filled with younger cells; and in the crocodile some of these cells contain a succession of cells, encased one within the other.

The following observations of Reichert on the yolk of the impregnated ovum of the frog were communicated to the author in manuscript.

" The yolk of the mature egg of the frog after fecundation consists of two different kinds of corpuscules, which are readily distinguished by their size. Those of the smaller kind occupy that part of the yolk in which the embryo first appears, and constitute the germinal layer or cumulus germinativus, which corresponds to the germ with the nucleus of the cicatricula in the hen's egg. (See page 1468.) The remainder of the yolk is entirely composed of the other kind of corpuscules, which are three or four times as large as the foregoing. These corpuscules composing the mass of the yolk, in which they are pressed very closely together, are visible with the naked eye, but may be distinguished very clearly with the aid of a lens. With a magnifying power of four hundred and fifty diameters they are seen to have a nearly circular outline, somewhat inclining to the oval. They appear nearly uniformly opaque and dark, and as if formed of numerous small globules, though at the periphery these globules are so closely pressed together that they project scarcely at all beyond the outline of the large corpuscules. If one of the corpuscules of the yolk is broken by pressure, the globules composing it are set free, and then appear nearly transparent, without shadows, but with very strong outlines, resembling in their entire aspect small globules. They are not, however, easily destroyed by pressure, and do not run one into the other. Their size is nearly uniform; a few only being remarkable for their size, and in these a slightly granular aspect can be perceived. Besides these globules, a number of much smaller granules of bright appearance, and endowed with a molecular motion, are set at liberty by the bursting of one of the yolk corpuscules. This description applies particularly to those corpuscules which lie in the centre of the yolk. Such as are situated nearer to the periphery, though they have the same general structure, yet are distinguished by having

Fig. 170.*



from two to four darker spots in their interior. (Fig. 170, A.) On crushing one of these corpuscules, there escape, in addition to the globules and granules already mentioned, several larger globules of a yellowish colour and granular aspect, sometimes surrounded by a lucid mass. These yellow globules were evidently the cause of the spotted appearance of the corpuscules. The nearer the part from which we take the corpuscules for observation is to the cumulus germinativus, the more distinct are the dark spots just described. The corpuscules at length appear nearly entirely composed of them, and thus there is a gradual transition to the smaller corpuscules of the cumulus germinativus, which seem to be the dark globules of the larger corpuscules in a free state. With the exception of the difference of size, these smaller corpuscules (fig. 170, c) exactly resemble the larger ones of the centre of the yolk. They are in greater part formed of the same small oil-like globules, but out of each of them a larger yellowish granular globule may be expressed (fig. 170, B), and the granules which present the molecular motion are much smaller, and appear quite dark. Several facts prove that these corpuscules are cells. As is so frequently the case when organic nucleated cells are quite filled with granular substance, the existence of a membranous wall and of a nucleus cannot be detected by the eye; but still it cannot fail to be remarked that the corpuscules, though lying in close contact with each other, retain their distinct form, and that the contour of each corpuscule is nearly even, although it is apparently composed of a mass of globules. Moreover, the yellowish granular globules, which may be expressed from many of these corpuscules, correspond exactly to the nuclei of cells; the granules, endowed with molecular motion, when forced from a corpuscule, escape gradually, as through a cleft, and the larger corpuscules resolve themselves into the smaller ones, just as parent cells produce smaller cells within their cavity. All doubt, however, as to these corpuscules being really cells is removed by the changes which the smaller ones, composing the 'cumulus germinativus,' are observed to undergo during the development of the embryo. The globular contents of the corpuscules are then seen to become in part absorbed, and the nucleus (which could previously be forced out of the corpuscule by pressure), as well as the membranous wall, becomes visible. (Fig. 170, c.)

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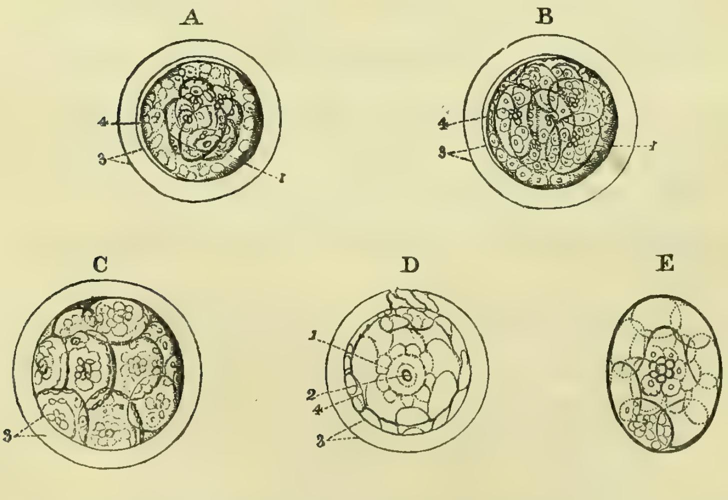
* [Fig. 170, cells from the fecundated ovum of the Frog, after Reichert. A, a cell from centre of the yolk. 1, the globular contents; 2, one of the larger globules, which is a young cell; 3, the membrane of the parent cell; B, one of the young cells set free by the bursting of a large cell. The membranous wall of this young cell is destroyed, and its nucleus, 4, is visible. c, cells from the most superficial layer of the cumulus germinativus; 1, a cell in which both nucleus and cell membrane are visible; 2, a cell in which the membrane is distinct, but the nucleus concealed by granular matter; 3, a cell in which these granular contents are nearly entirely absorbed, and a nucleus with nucleoli brought to view; 4, nuclei; 5, an intercellular space; 6, a cell in which neither the enveloping membrane nor the nucleus can be distinguished.]

"It appears, then, that the yolk of the frog's ovum consists of cells, whose nucleus and membranous wall are rendered invisible by their granular contents. Those cells which lie in the centre of the yolk are of large size, and contain no nucleus. In respect of the production of young cells, these are the least advanced. But nuclei afterwards appear in them; young cells become developed, and are recognised in those which are near to the periphery of the yolk, and most distinctly near the cumulus germinativus, as dark spots within the parent cells. The membranous wall of the parent cell now entirely disappears, and the young cells accumulate as the smaller yolk-cells in the cumulus germinativus, —a provision for the incipient development of the embryo. This process is continued as long as any yolk remains. Wherever any structures of the embryo are being formed, the smaller of the yolk-cells already developed by this process are applied to that purpose; while the place of the cells thus consumed is supplied by new ones from the centre of the yolk."

[The process described by Dr. Barry to take place in the yolk of the mammal's ovum, preparatory to and immediately after impregnation, is very remarkable. There appears to be a constant development of cells in the centre of the yolk. Each layer of these cells, while they enlarge and assume a flattened elliptic form, is pushed outwards by a new set developed internal to them. After impregnation, when the germinal vesicle has passed to the centre of the ovum, the develop-

Fig. 171.*



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* [Fig. 171 represents the structure of the yolk of the ovum of the rabbit, and the changes which take place in it immediately after impregnation. In A, B, and C, 1, indicates the layer of discoid elliptic cells developed around the germinal vesicle in the centre of the yolk; 3, the thick transparent membrane of the ovum, or the zona pellucida; and 4, the more internal non-persistent membrane surrounding the most external

ment of cells here described takes place in successive layers around that body. Each layer, on reaching the exterior of the yolk mass, is often seen to be circumscribed by a proper membrane, and at length undergoes liquefaction, the layer within it then supplying its place. (See fig. 171, A, B, C.) Fig. 171, D, is a scheme illustrative of this process. Each of the flattened elliptic cells also contain minute cells arranged concentrically around a pellucid point, and the contained cells again present a similar structure. (See fig. 171, E.) The same process, in fact, which has just been described as occurring in the yolk as a whole, seems to take place in all the cells met with in the ovum.] [Further information on this subject will be found in the Appendix.

3. *General plan of the development of fishes and the Amphibia.*

The germ first presents itself in the form of a thin stratum of yolk of definite extent—the "germinal membrane." Gradually this membrane extends itself over the whole surface of the yolk, so as to assume the form of a vesicle including the mass of yolk. In the ova of the Blennius viviparus the germinal membrane does not entirely surround the yolk until the embryo has been long formed (Rathke); while in the Cyprini it completely envelops the whole mass before any indication of the embryo can be discovered (Von Baer). The parts which form the axis of the embryo first show themselves. A groove-like depression appears at this part of the germ. Two ridges, the "laminæ dorsales," arise, one on each side of the groove. These ridges meet and unite in the middle line, and there constitute, according to the observation of previous embryotomists, the primary form of the vertebral column; while Reichert asserts that the "laminæ dorsales" are really parts of the nervous centres themselves. Along the middle line of the germ the "chorda dorsalis" is formed, a delicate continuous cord, which is afterwards surrounded by the lateral rudiments of the vertebræ, which make their appearance on each side.

The germinal membrane itself, according to the observations of Rathke and Von Baer, separates into two layers or laminæ, an internal and an external. The former—the mucous, or more correctly the organic, lamina—serves for the formation of the organic system of organs; whilst in the external serous, or animal lamina, the organs of the animal system of the body, (as the bones, muscles, and skin,) are developed. The heart appears between the internal and the external lamina of the germinal membrane in the form of a simple canal.

layer of yolk-cells. D, is an outline drawing of an ovum, more clearly illustrating the process. The cypher, 1, here indicates the germinal vesicle, and 2, the germinal spot. E, is a section showing the structure of one of the compound discoid cells by which in some states the germinal vesicle is surrounded. After Dr. Barry, Philos. Transact. 1840, Pt. ii. p. 535.]

Fig. 172.

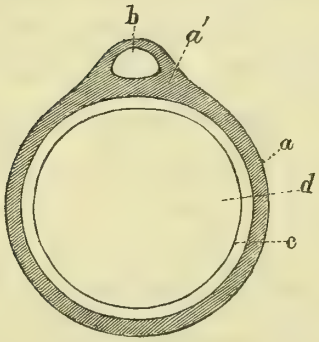

Figure 172 represents a perpendicular section through the embryo, germinal membrane, and yolk *a*, is the external, " serous, or animal layer," of the germinal membrane; *á*, one of the laminæ dorsales, or dorsal ridges; *b*, the vertebral canal; *c*, the internal or organic layer of the germinal membrane; and *d*, the yolk. We perceive that the animal part of the embryo here represents the section of a double tube, the organic part only the section of a single tube, and that the latter is contained within the lower tube of the animal layer. In the invertebrate classes, likewise, the body of the embryo is produced from a germinal membrane with an animal and an organic layer; but in the undeveloped state the two layers are simple vesicles which lie concentrically one within the other, and of which the abdominal part is in the articulata first formed, and the dorsal portion last. The section of the animal layer does not, as here, present the appearance of a double tube.

Those parts of the animal layer of the germinal membrane which form the upper tube or vertebral canal, the vertebral column and its muscles, have been named the " laminæ dorsales;" whilst those which form the inferior larger tube, and contain the organic system of parts, have been called the " laminæ abdominales," or " visceral plates." * The visceral plates are continuous along the sides of the trunk; but at the head they, at a very early period, assume the form of bands or arches descending from the cerebral capsule, and uniting at their lower extremity. There being several of these arches, a series of clefts occur between them on each side of the neck. The oral cavity subsequently lies between the most anterior of the arches and the cerebral capsule. These arches and clefts which are observed in the embryos of all vertebrate animals, are the " branchial arches and clefts" of Rathke, and the " visceral arches" and " visceral clefts" of Reichert.

The principal modifications of the process of development met with in the classes of Fishes and Amphibia are the following:—

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* A different application of these terms, however, has recently been introduced by Rathke, (Müller's Archiv. 1839, p. 361; and Entwickelungs-geschichte der Natter, p. 61.) To the very thin membranous part of the abdominal walls in the embryo of all the vertebrate classes, he gives the name " Membrana reuniens inferior," and to the corresponding part in the dorsal region the name of " Membrana reuniens superior;" whilst he reserves the terms " laminæ abdominales," and " laminæ dorsales," for the thicker parts of the parietes of the abdominal and dorsal regions of the embryo, which, advancing from each side, at length meet above and below in the middle line. When these thicker laminæ have thus united and enclosed the cavities to which they belong, the " membranæ reunientes" have lost their office.

I. The Amphibia occupy the lowest place, since in them the whole germinal membrane enters into the formation of the embryo. When the structures of the axis of the embryo have gradually become developed, the cephalic and the caudal portion project above the level of the rest of the germinal membrane, and the sac which the latter forms depends from the abdominal surface of the embryo. The external layer of this sac is continuous with the central axis of the embryo, and with the inferior part of the head and caudal extremity. From it are produced the parietes of the trunk, which are part of the animal system, and are connected with the structures of the axis. The internal layer of the sac has the form of a globular vesicle, and is not immediately connected with the vertebral column and other parts of the axis. This internal vesicle which contains the yolk is the first state of the intestinal cavity. It subsequently assumes the tubular form, and develops the appendages of the canal, separating at the same time into the different coats of the intestines. Invested externally by the animal layer of the germinal membrane, or the parietes of the trunk, this internal sac gradually assumes more and more the elongated form. Openings appear at the anterior and posterior extremity of the sac, thus elongated, at the points where it comes into relation with the animal system. These openings are the mouth and anus. The embryo of the Amphibia, therefore, passes gradually from the state, represented in figure 173, to that shown in figure 174. Here A and *a* represent respectively the animal part of the embryo, and the animal layer of the germinal membrane; A, the structures of the axis being continuous with the parietes of the trunk or abdominal plates, *a*; *b*, indicates the abdominal part of the embryo, viz. the alimentary cavity or canal; *x* is the heart.

Fig. 173.

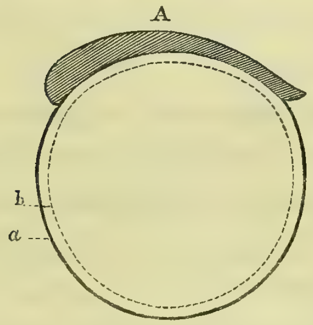
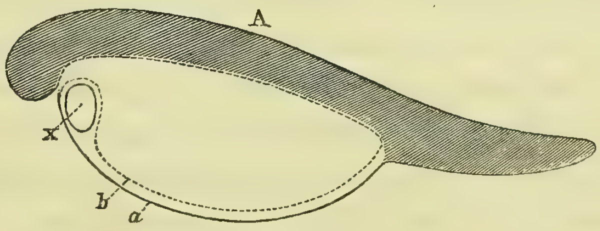


Fig. 174.



This seems to be the general plan of development of some of the Amphibia, but not of all. In the Bufo obstetricans, according to my observation,* the abdominal sac consists of an animal portion, and of an organic portion, and the intestinal canal is distinctly developed from the internal organic layer, and has already a convoluted form before the

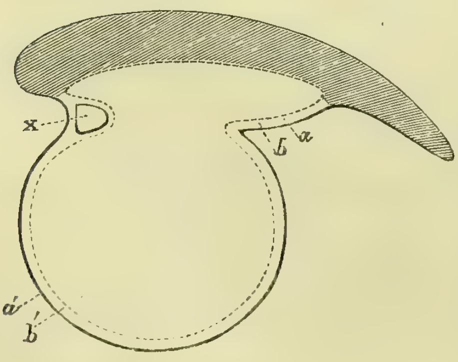
* See the figures in my work on the structure of glands (De Glandularum Penitiori Structurâ. Taf. x. fig. 6—9).

embryo leaves the ovum. (This batrachian has also a complete branchial circulation before its escape from the egg.) In the frog, however, the foregoing scheme of development is by no means applicable. In the ovum of the frog there is no germinal membrane with two distinct layers; but all the structures of the embryo are formed in succession from the yolk. According to Reichert, even when the embryo of the frog has left the ovum, the intestine is still not marked off from the mass of the yolk. The organic system of the body is here not formed until long after the complete development of the animal system.

II. Next in simplicity to the process of development of the Amphibia, we must place that presented by certain fishes. In these the external layer of the germinal membrane becomes entirely converted into the parietes of the trunk, but only part of the internal layer goes to form the intestinal canal; while the other portion is separated by a constriction, and forms a vitellary sac appended to the intestine. The constricted part forms a canal of communication between the cavity of the intestine and that of the sac containing the yolk. This yolk-bag, however, does not hang to the exterior of the body, but is included, together with the intestinal canal, within the parietes of the body, formed from the external layer of the germinal membrane. This "internal yolk-sac" is met with, according to Von Baer's observations, in the Cyprini, and, according to Rathke, in the perch and salmon likewise. In the Cyprinus family, the internal yolk-sac still exists when the young fish escapes from the egg, but has already much diminished in size; and it afterwards gradually disappears entirely. The duct of communication between this internal yolk-sac and the small intestine may be termed the ductus vitello-intestinalis internus.

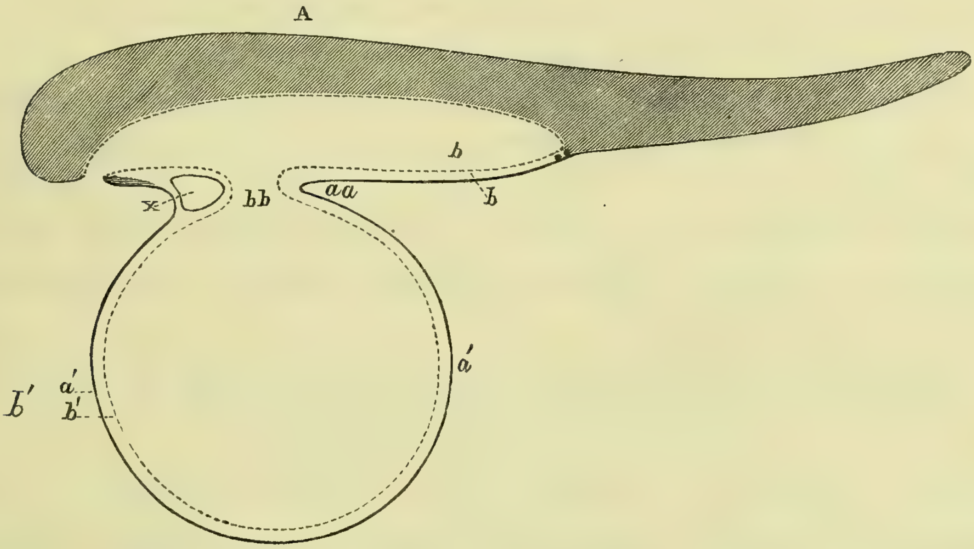
III. A third modification of the process of development is presented to us in those fishes which have an external yolk-sac, lying in front of the abdominal parietes of the embryo, and formed of a part both of the internal layer and of the external layer of the germinal membrane. Thus, in figure 175, A, marks the structures of the axis of the embryo: *a*, the abdominal parietes or plates; *a′*, the part of the external layer of the germinal membrane, which has become separated by a constriction from that part, forming the parietes of the body of the embryo, and which constitutes the external coat of the yolk-sac; *b*, that part of the internal layer of the germinal membrane which is converted into the intestine; *b′*, that part of the same layer which forms the yolk-sac;

Fig. 175.



and *x*, the situation of the heart between the animal, and the organic layer of the germinal membrane. In this form, therefore, the entire embryo, with the animal and organic parts of its trunk, becomes separated by a constriction from the remainder of the vesicle or sac formed by the germinal membrane; and as the separation by constriction gradually increases, the sac comes to hang as an appendage to the body of the embryo (see fig. 176). The sac is appended in this case to the most anterior part of the abdominal parietes, close beneath the heart. The external coat of this appended sac (*a′*, in fig. 176) is called the umbilical sac. The part at which it is connected with the parietes of the abdomen is the umbilicus, *a a*. The internal layer or coat of the appendage is the proper vitellary sac, *b′*, in which the yolk is contained, and from which the ductus vitello-intestinalis (in this case "externus"), *b b*, extends inwards through the umbilicus to the small intestine of the embryo. The part of the internal layer of the germinal membrane which passes through the umbilicus may be called the umbilicus intestinalis. Such is the disposition of the parts, according to Rathke's researches, in Blennius viviparus, and Cottus gobio. Upon the yolk-sac are distributed the vasa omphalo-mesaraica, which accompany the ductus vitello-intestinalis through the umbilicus. The umbilical sac, with the yolk-sac which it contains, diminishes in size in proportion as the embryo becomes developed, and is at length wholly absorbed.

Fig. 176.



IV. Another modification of the process occurs in the plagiostomatous fishes, the Sharks and Rays. At a certain period in the progress of their development the umbilical sac appended to their abdomen, generally by a long pedicle, contains a yolk-sac, and omphalo-mesenteric vessels. The duct of this yolk-sac, or ductus vitello-intestinalis, passes through the umbilicus, and unites with the superior extremity of the intestinum valvulare, into which, as Stenonis first observed, the bile likewise is poured. In most of the Sharks and Rays, however, whether they are developed within the uterus, or not, there exists at a certain period, in addition to this external yolk-sac, an internal yolk-sac, which lies within the abdominal cavity.* This is a large cæcal diverticulum of the ductus vitello-intestinalis towards one side, which fills the greater part of the cavity of the abdomen.† When the embryo has attained its maturity, the umbilical sac, with the external yolk-sac which it contains, gradually diminishes in size, and at length disappears entirely by absorption. But in embryos which are fully developed the internal yolk-sac is still found, though its size has undergone diminution. In some of the Shark family the ductus umbilicalis is beset in its entire length with villi; this state was observed by Cuvier in Carcharias,‡ and by Leuckart in *Zygœna*. According to my observations the internal yolk-sac exists in addition to the external one in all Sharks and Rays, whether oviparous or viviparous, with the exception of those Sharks (the genus Carcharias), in which the external yolk-sac becomes transformed into a placenta fœtalis, and firmly connected with a placenta uterina of the parent fish.§

4. *The process of development exemplified in the formation of the principal organs in the embryo of the frog.*

In the foregoing pages we have given a concise exposition of the principal modifications of the general plan of development, which are met with in fishes and Amphibia. A detailed account of the process of development as it occurs in each of the classes of animals, corresponding to their modifications, would not accord with the object of this work. We must be content with illustrating the process by one example. Reichert's observations on the development of the embryo of the frog seem peculiarly adapted to furnish this illustration; for the researches of previous writers into the mode of development of fishes and Amphibia, though very valuable, were instituted before Schwann discovered the important part played by the organic cells in the formation of the embryo. Moreover, the process of development presents perhaps more peculiarities in the frog than in any other animal of the classes of fishes and Amphibia,—departs more from the general plan, and is consequently most interesting, as tending to show us what is, and what is not, essential to the process.

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* This internal yolk-sac had been seen by Aristotle. Speaking of the Sharks, he says, (Hist. Anim. 6. 10,) "In dissecting the fœtus we still find the egg-like mass of nutriment, even when the egg is no longer present." Ἡ δὲ τροφὴ ἀνατεμνομένου, κἂν μηκέτι ἔχῃ τὸ ὠὸν, ὠοειδής.

† This structure is represented by Collins, in his System of Anatomy, 1685. Tab. 33.

‡ Correctly Scoliodon (of Müller and Henle), a subgenus of Carcharias. In the Carcharias with serrate teeth (Prionodon of Müller and Henle), the umbilical duct is devoid of villi, and quite smooth.

§ On the development of the Amphibia consult Rusconi, Développement de la grenouille commune. Milan, 1826; et Amours des Salamandres Aquatiques. Milan, 1821; et Von Baer, in Burdach's Physiologie, Bd. ii. On the development of fishes see Rathke on the Blennius viviparus, in Abhandlungen zur Bildungs und Entwickelungs-geschichte, ii. Leipz. 1833; Von Baer, Untersuchungen über die Entwickelungs-geschichte der Fische. Leipz. 1835; Rathke, Beiträge zur Geschichte der Thierwelt, iv. (Haifische); Dr. J. Davy, Philos. Transact. 1834, p. 2 (on the Torpedo); and J. Müller, in Bericht über die zur Bekanntmachung geeigneten Verhandlungen der K. Acad. der Wissensch. zu Berlin, 1839, Febr.

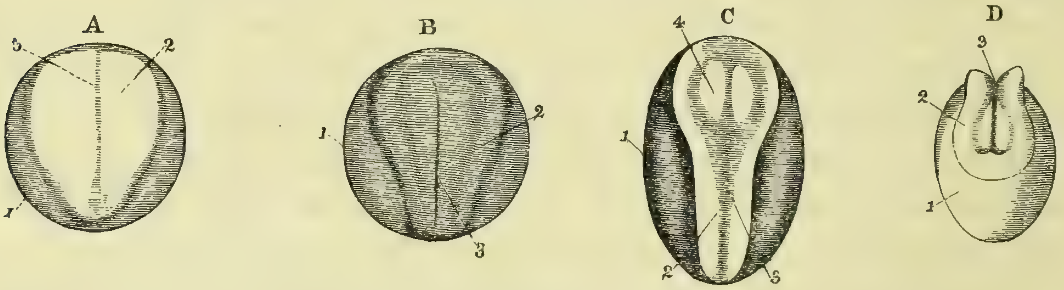
We shall find, however, that even in birds, according to Reichert's observations, the different systems of organs are not developed in such a regular manner, from different lamellæ of the germinal membrane, as has hitherto been supposed.

Reichert remarks in the first place, that " in following the series of metamorphoses presented by the embryo of the frog during its development, the observer must throw aside all preconceived notions derived from the history of the process of development in other animals, and that he must not expect to find a germinal membrane with a serous, a vascular, and a mucous layer, such as are ordinarily described. The first rudiment of the embryo is formed upon the cumulus germinativus, described at page 1512, which corresponds to the cumulus germinativus or nucleus of the cicatricula in the hen's egg (see page 1468). The germinal disk from which the germinal membrane is afterwards developed in the ovum of the hen, does not exist in that of the frog. It may be remarked as a general law, that the development of an organ, or system of organs, in the embryo always takes place by the direct aggregation of those smaller cells of the yolk, which are formed at first merely in the cumulus germinativus, but afterwards in the whole periphery of the yolk, so as to constitute its cortical layer. The cells composing the newly-formed structure of the embryo are therefore originally identical with those contained first in the cumulus germinativus, and afterwards in the cortical layer of the yolk. From the organisation of the yolk,—from the circumstance of the smaller cells adapted for the immediate construction of the embryo always existing merely at its surface,—it follows that the mass of the yolk must be gradually consumed in successive strata from without inwards. The first of the structures of the embryo which is developed from the yolk is the central part of the animal nervous system; the last is the mucous membrane of the intestine, the representative of vegetative or organic life.

Membrane investing the yolk during the development of the embryo.—The formation of this membrane is the first act of the process of development. It is produced by the separation of a single layer of cells upon the surface of the cumulus germinativus, from the mass beneath. In consequence of the deposition of a dark pigment in some of the cells composing it, it in the frog very soon appears coloured. This membrane rapidly extends beyond the limits of the cumulus, and has invested the surface of the entire yolk before any trace of the embryo is visible. Its extension is accompanied by the constant development of small cells upon the surface of the yolk, specially destined for its formation. Consequently when this investing membrane is completely formed, the periphery of the yolk has acquired a continuous stratum of those smaller cells which are prepared for the development of the embryo, and which are accumulated in larger number in the cumulus. By the time that this investing membrane is formed, the former vitellary membrane of the ovum has entirely disappeared.

Primary form of the animal system of organs.—As soon as the investing membrane is completed, the development of the embryo from the yolk commences by the formation of the rudiments of the animal system. The chorda dorsalis, and on each side of it the rudiments of the central parts of the nervous system, first appear. These parts may be distinguished externally immediately over the cumulus germinativus, where the investing membrane was first formed. A space of nearly oval form is there seen, in which the investing membrane has a paler colour. Through the middle of this space, which occupies about a third of the surface of the yolk, and which is rather wider at the end corresponding to the cephalic extremity of the future embryo, a narrow and shallow furrow runs in the longitudinal direction. (See fig. 177, A and B.)

Fig. 177.*



This furrow indicates the course of the chorda dorsalis; and the parts of the surface which lie on each side of it correspond to the rudiments of the central organs of the nervous system. In a transverse section both these structures are seen to be formed of cells newly deposited at the surface of the cumulus germinativus, and in close contact with the "investing membrane." A distinct line of separation or cleft is visible between these rudiments of the embryonic animal system, and the rest of the cumulus germinativus; and this again is now seen to be separated from the central mass of the yolk by an apparent chasm, while at its circumference it still maintains a direct connection with the other yolk-cells.

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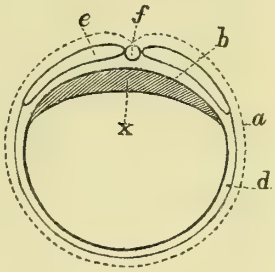
* [Fig. 177 represents the development of the rudimental nervous system in the ovum in the frog; after Reichert. 1, indicates the resisting membrane which has extended over the entire surface of the yolk. 2, the rudimental lateral halves of the nervous centres. 3, the median furrow. 4, part of the nervous centres corresponding to the future brain.]

Fig. 178.



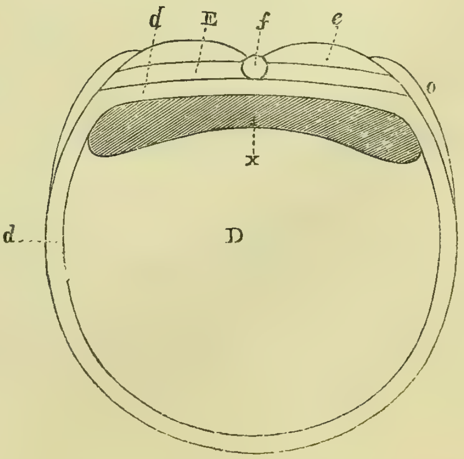
In figure 178, the dotted line *a* represents the investing membrane; *b,* the cumulus germinativus; *d,* the cortical layer of yolk-cells continuous with the cumulus; *e,* the rudiments of the central organs of the nervous system divided transversely; *f,* the chorda dorsalis; and *x,* the chasm in the yolk beneath the cumulus.

The cells composing these rudimentary structures of the embryo are all identical with the smaller yolk-cells before described as being developed in preparation for the formation of the embryo. In the " investing membrane," and wherever they are deposited in a form approaching to that of a single membranous layer, they acquire the polyhedric shape.

As development progresses, the lateral halves of the rudimentary nervous centres, increasing in thickness, become drawn towards each other, and towards the median line of the embryo. (See fig. 177, C and D.) They thus form two ridges, one on each side of the chorda dorsalis, which gradually become more and more prominent, and render the median furrow proportionally deeper. These ridges have been erroneously regarded as the rudiments of the vertebral system, and have therefore been called the dorsal plates, while the depression which they bound has been named the dorsal groove. This groove, or furrow, is wider at the cephalic extremity of the embryo than posteriorly; for the lateral halves of the rudimentary nervous system diverge at the part where the brain is to be formed, and after describing an arch on each side, meet again in the middle line. In the dorsal furrow a delicate connecting membrane becomes visible; and soon afterwards, in the cephalic portion, the three main divisions of the brain appear. At each side of the brain, and intimately connected with it, two oval masses of cells are seen, placed one in front of the other. These are the first rudiments of the eye and ear.

Besides the structures here described, another part of the embryo has, at this period, become isolated from the cumulus germinativus, namely, the true vertebral system. This, like the rudiments of the nervous centres, consists at first of two membrane-like laminæ of the cumulus, which lie at each side of the chorda dorsalis, beneath the central organs of the nervous system, and so concealed by the latter parts as not to be visible externally, and to be rendered apparent only by a transverse section. There are, as yet, no signs of vertebræ. In figure 179, *b* is the cumulus; *d,* the cortical layer of

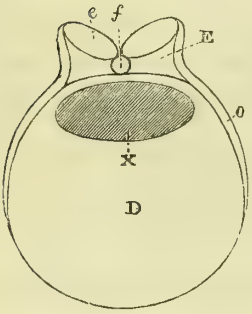
Fig. 179.



the yolk; *e*, the nervous centres; *f*, the chorda dorsalis; E, the dorsal or vertebral plates; *x*, the chasm in the yolk beneath the cumulus germinativus; and D, the yolk.

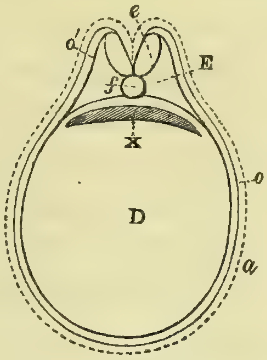
About the same time, also, the development of a system commences, which, after sundry metamorphoses, becomes at length the cutis of the animal. This may be called the cutaneous system, the precursor of the future parietes of the body, since it is of importance in the formation of the animal structures which constitute the parietes of the body of the embryo. This rudimentary cutaneous system lying beneath the "investing membrane," is seen most distinctly at that part where the external border of the rudimentary nervous centres on each side comes into relation with the rest of the yolk. It is indicated in figures 179 and 180 by the letter *o*. When it first appears, it forms a membranous layer of cells, which can be traced for a certain distance upon the external surface of the rudimentary nervous centres, as well as in the contrary direction over a small portion of the yolk; the cells composing it are polyhedral. The development of the cutaneous system commences at the external border of the cumulus germinativus, where this mass of formative cells is continuous with the other cells of the yolk; and it becomes extended inferiorly by the separation of the most superficial layer of cells from the surface of the yolk. Before the cutaneous systems of the two sides can meet, they have to extend by this mode of growth over a great extent of surface.

Fig. 180.



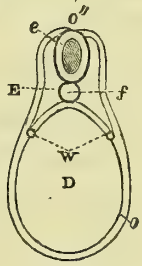
The ovulum gradually assumes a more and more elongated form: at the same time, the lateral halves of the rudimentary nervous centres approach each other more closely, and at length form a crest-like elevation upon the surface of the yolk, which has been regarded as the rudimentary vertebral column. The part of the embryo from which the true vertebral column is afterwards developed, lies beneath this crest. In proportion, however, as the lateral halves of the nervous centres become approximated, the rudimentary vertebral plates, increasing in size, become visible at their outer border. The vertebral plates thus come into relation with the cutaneous system, and, with the protection and aid of this system, proceed to the formation of the two tubes of the vertebral system, by the development of the dorsal and visceral plates. When the formation of these plates has commenced, they extend like two processes on each side from the body of the vertebral plate, one upwards and the other downwards. Soon afterwards the symmetrical segments of the vertebral column, the lateral halves of the vertebræ, begin to show themselves in the rudimentary vertebral plates. In figure 181, the dotted line *a* represents (as in figure 178) the dark investing membrane of the ovum and embryo; *e*, the rudimentary nervous centres; *f*, the chorda dorsalis; E, the rudimentary vertebral plates, with their upward and downward prolongations, the dorsal and visceral laminæ; *o*, the cutaneous system; *x*, the chasm in the yolk beneath the cumulus germinativus; and D, the yolk.

Fig. 181.



The lateral halves of the rudimentary central nervous system now coalesce by their upper borders; their inferior borders had previously become united. The dorsal groove, with the black investing membrane lining it, is thus converted into a closed canal. At this period, therefore, the central nervous system has the form of a tube, which is wider at the cephalic extremity, where its cavity remains through life as the cerebral ventricles. The walls of this tube are thicker at the sides than above and below, and in its cavity are contained the remains of the portion of the dark investing membrane which lined the dorsal groove. In figure 182, *e*, represents the central nervous system enclosing a canal; E, the vertebral system; *f*, the chorda dorsalis; and *o*, *o″*, the cutaneous system. The cutaneous system has extended beneath the investing membrane, over the whole surface of the yolk. Before the dorsal and visceral plates have met from opposite sides, so as to complete the upper and lower tubes, the cutaneous system serves to supply their deficiency; hence the part of the cutaneous system which unites the dorsal plates has received from Rathke the name of membrana reuniens superior; and that part of it by which the visceral plates of opposite sides are connected, the name of membrana reuniens inferior. In figure 182, *o*, is the membrana reuniens inferior; *o″*, the memb. reun. superior.

Fig. 182.



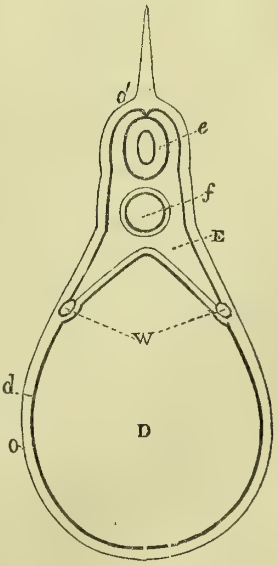
The embryo of the frog leaves the ovum at an earlier period than the fœtus of any other vertebrate animal; namely, as soon as the animal system of organs has been formed, though only in a rudimentary condition. The lateral halves of the rudimentary nervous centres have united, and the superior vertebral tube has become nearly closed in the trunk by the union of the dorsal laminæ, or arches, and the inferior vertebral tube at the head by two visceral laminæ, or arches; while in other parts these tubes are completed by the "connecting membranes." The tail of the tadpole is already distinctly visible. The entire embryo is invested by the cutaneous system, which plays so important a part in the early stages of development, and, externally to this, by the original "investing membrane." As a means of attachment, two suckers have been developed from the cutaneous system upon the first visceral arches.

Nutritive system for the organic life of the embryo. — Sanguiniferous system.—The development of the systems and organs destined for the common nutrition of the aggregated cells composing the embryo, does not commence until the animal system of organs, and thereby the external form of the embryo, are essentially completed. The development of the parts belonging to the animal system was effected by the mere vegetative endowment of the cells, without the aid of a vascular or sanguiniferous system, which is formed in the frog at a remarkably late period. The chasm already mentioned as existing in the yolk, immediately beneath the cumulus germinativus, persists as long as the rudiments of the animal system are being formed. Their development consumes so much of the cumulus, that afterwards only a thin layer of cells remains. The chasm in the yolk now disappears, and the remaining layer of the cells of the cumulus comes into close contact with the central mass of the yolk. The yolk then contained in the trunk of the embryo is entirely surrounded by an uniform, single, cortical layer of cells. In the head, on the contrary, the chasm is increased in size by the retreat of the yolk towards the abdomen, and the cavity of the mouth is thus formed. The single layer of cells which remained from the cumulus germinativus lies at the under surface of the basis of the cranium, and has also extended itself over the inner surface of the two visceral arches of the head. A complete lining membrane of the oral cavity is thus produced. A portion of the main mass of the yolk contained in the abdominal cavity projects more anteriorly than the rest of the mass, and is applied to the formation of the heart. The heart itself is developed from the middle of the lower part of this projecting mass, and the aortic arches at its sides. In their first rudimentary state these organs are solid masses; at a later period they acquire a tubular cavity, in which are seen the blood corpuscules or cells. The blood corpuscules are at this period quite round, and contain each a nucleus with nucleoli, and a granular matter in the cavity of the cell. A special cavity for the heart, distinct from that of the abdomen, and invested internally with a layer of epithelium (the pericardium), is also produced. With the aortic arches there are developed three branchial arches, which lie in the second visceral or, so-called, branchial cleft. From the formative substance of the branchial arches the branchiæ themselves are formed. These branchial arches and branchiæ are, together with the future cutis, produced from that embryonic structure which, in the preceding pages, has been termed the cutaneous system.

While the heart is connected anteriorly with the branchiæ through the medium of the aortic arches, its posterior extremity sends ramifications directly into the anterior part of the mass of yolk contained in the cavity of the abdomen. This part of the yolk is soon afterwards seen to isolate itself from the rest of that substance, and to become an independent body. It is the rudimentary mass from which the liver and pancreas are subsequently formed, but which as yet presents no indication of a division into two organs. The liver and pancreas are thus developed in the frog, from the mass of the yolk, before any trace of a digestive canal is perceptible in the abdominal cavity. The generation of young cells within parent cells is nowhere so distinctly manifest as in this formative mass of the liver and pancreas. The active development of cells which here takes place, is probably connected with the process of sanguification, since the phenomena, of which the area vasculosa of the germinal membrane of other animals is the seat, are not observed in the frog. The same direct aggregation of the yolk-cells contained in the abdominal cavity, which produced the liver and pancreas, also gives rise to the Wolffian bodies. These organs are situated in the place pointed out by Müller, close to the branchial apparatus, and their excretory ducts run along the abdominal cavity to the temporary anal opening formed by the cutaneous system. In figures 182 and 183 the situation of these ducts is shown; their transverse section being indicated by the letter w.

Further progress of the development of the animal system.—The embryo of the frog assumes first a fish-like form. The fin-like appendage and the horny plates in the mouth of the tadpole are developed from the cutaneous system. This system, however, is already reduced to little more than a protecting investment of the vertebral system, or of the animal parietes of the trunk. At the posterior part of the body merely, it still acts as membrana reuniens inferior, and forms the temporary anal opening. The central organ of the nervous system loses more and more the tubular form, in consequence of the thickening of its lateral halves; and the part of the dark investing membrane formerly contained in it disappears. The peripheral nervous system also becomes visible. In figure 183, *e* represents the central organ of the nervous system; *f*, the chorda dorsalis; E, the vertebral system, with its superior and inferior processes, the dorsal and visceral plates; *o*, *o*′, the cutaneous system, *o* being the membrana reuniens inferior; D, the yolk, contained in the simple abdominal cavity, no digestive canal being yet present; and *d*, the cortical layer of the yolk.

Fig. 183.



Digestive canal.—The development of the intestine, or digestive canal, does not commence in the frog until after the animal system is completed, and the sanguiniferous system has received its rudimentary form. In the earliest periods of development the globular matter contained in the formative cells themselves furnished the nutritive material; and afterwards, the liver and pancreas, or the rudimentary mass from which they are produced, conveyed the nutriment into the sanguiniferous system. No digestion was as yet required. The tadpole at this period appears on a superficial view fully formed. It is furnished with external gills and moves with great vivacity, but it takes no food. The intestinal canal, destined for the reception of foreign nutritive substances, is formed in the following manner:—The remaining mass of the yolk occupies now the great posterior division of the visceral cavity of the trunk, extending from the pharynx in front, and completely filling the rest of the cavity, with the exception of the space occupied by the rudiment of the liver and pancreas and the heart. Consequently, it lies in contact with the pharyngeal opening of the mouth, with the margin of the membrane investing the oral cavity, and with the rudimentary mass of the liver and pancreas anteriorly; with the cutaneous system, or the membrana reuniens inferior, posteriorly, inferiorly and laterally; and with the vertebral column, the visceral plates and the Wolffian bodies attached to them, superiorly (see fig. 183). The yolk, however, lies quite free, and is not held together by any special membrane. All the cells of the yolk are now found to contain young cells in their cavity, and on the surface of the mass these young cells are set free and prepared for the development of fresh organs. In the frog and water salamander (Triton), and probably in all those lower vertebrate animals, in which successive layers of the yolk are employed in the development of the embryo, the intestine is first formed as a simple tube, destitute of mucous membrane; this membrane being subsequently added, as the last product developed from the yolk.

The membrane of the intestine.—The primitive membrane of the intestine is formed by the most superficial layer of the cells of the yolk, on each side, becoming separated in a membranous form. The membrane thus produced lies as an inclined roof-like covering over the yolk, and is firmly attached by its superior border along the vertebral column; so that there hang from the vertebral column two membranous laminæ (the parts described by Von Baer in the chick as the intestinal laminæ). Very soon these laminæ meet and unite inferiorly also, and thus include the whole yolk. The embryonic membrana intestinalis now forms a sac of a flattened oval shape in the abdominal cavity. Posteriorly, it communicates with the exterior by the temporary and orifice in the skin, together with the excretory ducts of the Wolffian bodies. Anteriorly, it extends to the internal or pharyngeal opening of the oral cavity, and there becomes directly continuous with the lining membrane of that cavity.

The latter, consequently, must be regarded as the first-formed cephalic portion of the intestinal membrane. The primary membrane of the intestine is originally constituted of the simple cells of the yolk. Within these, young cells are afterwards developed. When the peculiar form of the intestine in the tadpole is tolerably distinct, the cells composing the intestinal membrane undergo two different kinds of changes: first, they become converted in the abdominal portion of the canal into primitive muscular fasciculi, which run for the most part transversely; and secondly, they are transformed into the glands, the secretion of which effects the digestion of the food. Lastly, a dense vascular net-work becomes developed in the parietes of the canal; and here also the blood-cells contain a finely granular matter, which is sometimes confined to the periphery of the nucleus, and sometimes occupies the entire cell.

The mucous membrane.—When the intestine has acquired the form of a small, spirally-convoluted tube, the remains of the yolk lie within the canal, forming a loose, but tolerably thick crust upon its internal surface, and leaving a small cavity in the middle of the canal. This crust is composed chiefly of the smaller yolk cells; the large cells of the yolk exist in it in very small number. It extends no farther than the abdominal part of the digestive canal. The yolk had retired from the cephalic portion of the cavity at a much earlier period, and the crust of cells is also not found there at the time of which we are speaking. As the intestine increases in length, the crust of cells on its inner surface grows thinner, and the cavity increases in diameter. At length this remaining yolk becomes so extended upon the inner surface of the intestine as to form only a single layer of yolk-cells: and this layer now becomes converted into the structure which must be regarded as the mucous membrane. The cells of this structure soon change their form; they become elongated in the direction of the radius of the cavity of the intestine, and acquire in part a conical, and in part a cylindrical shape, the apices of the cones being directed outwards. A nucleus is distinctly visible in each of these elongated cells; and by degrees they become filled with fat-like globules. This layer of the intestinal parietes is destitute of vessels. The intestine now consists of two tubes,—the tube of the muscular coat and that of the mucous coat, with a layer of glands between them. It is remarkable that this mucous or assimilating coat of the intestine exists only in the abdominal portion of the canal. In its structure it resembles most closely the so-called epithelium of the intestine. But the term epithelium is here avoided, since this coat is evidently the assimilating organ of the intestine, no other mucous membrane existing in the intestine of the tadpole. Indeed, the cells of the so-named epithelium in fully developed animals may have a higher function than that generally ascribed to epithelium; they may be the active elements in the processes of absorption and assimilation.

The mesentery.—At first no mesentery exists. The primary form of the digestive or intestinal sac corresponded to that of the mass of yolk contained in the abdominal cavity, and had a somewhat prominent border attached to the vertebral column. In proportion, however, as the digestive sac becomes elongated, the yolk and the intestinal membrane enclosing it must necessarily be removed from that part; and this is more particularly the case at the middle portion of the intestine which assumes the spirally convoluted form. The two laminæ of the primary intestinal membrane, which are attached along the vertebral column (mesenteric plates), gradually approach, and come into contact with each other to an extent corresponding with the distance to which the intestine is removed from the vertebral column, and then coalesce so as to form a band connecting those parts,—the mesentery. When the development of the different tissues in the primitive intestinal membrane takes place, a non-vascular layer of epithelium separates from the free external surface of that membrane. The same takes place on the surface of all the other structures in the abdominal cavity; and thus is produced the peritoneum. The formative mass between the two epithelium layers of the mesentery serves for the development of vessels, nerves and the spleen. While, therefore, the non-vascular layers of cells seem to serve merely as a band of attachment, the principal mass of the mesentery represents the essential connexion between the systems of animal and vegetative life. The pericardium surrounding the heart, and the arachnoid, and all the serous sacs met with in other animals, are formed in the same way as the peritoneum.

When the intestinal canal is fully developed, the yolk is completely exhausted, and the tadpole organism of the frog perfect. The external gills have at the same time disappeared, and the internal gills have become developed. All the new parts which are developed during the subsequent metamorphosis of the larva, result from the production of new formative cells at determinate parts of the organism. Thus are formed the extremities of the young frog; the anterior part of which lie concealed within the branchial cavity. This cavity is formed by the union of the membranous branchial operculum, developed for the protection of the branchiæ, with the anterior part of the body of the tadpole, except at one point, where a small round branchial aperture is left. The anterior extremities are not set free until the branchial apparatus becomes atrophied, and the pulmonary respiration commences. As soon as the vertebral system of the animal is fully developed, the "cutaneous system" retains no other function than that of forming the external investment of the whole animal. The fin-like appendages, the membranæ reunientes, the cutaneous temporary anal orifice, and the horny lamellæ of the mouth, cease to exist. The lungs do not arise from the same embryonic system which produced the branchiæ. The reduction of the cutaneous system to the mere cutis is attended by the atrophy and disappearance of the embryonic "investing membrane," and by the development of the epidermis, which may sometimes be detected beneath the "investing membrane." The development of the lungs commences at an earlier period, when the intestine has assumed merely a sigmoid curvature. They appear at the sides of that canal at the point where it enters the cephalic part of the larva; but they are not developed from the intestinal canal itself. The kidneys are formed about the middle period of larval life. The structure of the intestinal canal of the larva also undergoes great changes, connected with changes in the nature of the food taken. The generative organs are at first wholly wanting, their development commences simultaneously with that of the extremities.

CHAPTER II.

DEVELOPMENT OF BIRDS AND REPTILES.

We have seen that fishes and Amphibia are developed according to one type, from which they do not in any essential respect depart, and are distinguished from all the other vertebrata by the want of the Amnion and Allantois. In the same manner, birds and reptiles (including the serpents, lizards, crocodiles, and turtles, and tortoises) agree in the main features of the process by which they are formed from the ovum, and all are furnished with both amnion and allantois. These membranes had been observed by Aristotle * in the embryo of birds. He distinguished a membrane which contained the yolk, a second which surrounded the embryo (the amnion), and a third which surrounded both the others, and also the fluid which existed between them. This third membrane he named the chorion. He recognised vessels also both in the membrane containing the yolk and in the chorion. In birds and reptiles there is no internal vitellary sac, as in some fishes, but the external vitellary sac is at length received through the umbilicus into the abdominal cavity. This fact also had been observed in birds by Aristotle. Moreover, it is peculiar to the animals of which we are now about to consider the development, that the umbilical sac, which in fishes contains the vitellary sac, and is continuous with the parietes of the trunk, is absent; the corresponding lamina surrounding the yolk being absorbed at an early period.†

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* Hist. Animal. iv. 3.

† The physiological differences in the process of development between the Amphibia and Reptiles are sufficient to justify the complete separation of these two classes of animals, independently of the essential anatomical characters which distinguish them.—(See J. Müller Tiedemann's Zeitschrift, iv. 2.)

The process of division and subdivision of the yolk, observed to precede the formation of the embryo in Amphibia and fishes, appears likewise not to take place in reptiles and birds.

The process of development in these classes will now be described more particularly, as it is presented to us in birds; the different stages of the process in this class having been followed most accurately by C. F. Wolff, Pander, and Von Baer.* The general view of the subject will be drawn from the classical works of those observers; but the account of the details of the process, and of the share which the cells of the yolk have in it, will be extracted from Reichert's manuscript statement of his more recent researches.

1. *General view of the process of development in birds.*

Development takes place in the ovum of birds under the influence of a temperature adapted to the life of a delicate warm-blooded animal, — namely, at a temperature varying from 95° to 104° Fahr. During the process of development, an evaporation of water, such as this temperature is calculated to induce, takes place from the surface of the egg; but this evaporation of water is not greater than would occur at the same heat were the egg not impregnated. As a consequence of this loss of its watery part, the white retires from the larger extremity of the egg, and a space is left there which becomes occupied by air entering through the pores of the shell. The air contained in this space has very nearly the same composition as common atmospheric air.

The first change which the "germ" presents in consequence of incubation, is its uniform extension at its margin. While thus enlarging, the "germinal membrane" for a time preserves its original thickness, and its outline remains circular. The influence of the developing germ upon the yolk gives rise to the appearance of several circular streaks — the "halones"— around the germinal membrane. These belong, not to the germinal membrane, but to the yolk itself. The "nucleus cicatriculæ," which lies beneath the centre of the germinal membrane, remains unchanged, and does not enter into any closer connection with that membrane. After the lapse of several hours, the middle portion of the germinal membrane becomes more transparent, and forms the "area pellucida." In this space, which at first has the form of an elongated ellipsis, but afterwards becomes more pear-shaped, the embryo appears. In figure 184, *a* indicates the "transparent area" or "area pellucida." All the surrounding portion of the germinal membrane is opaque. The entire germinal membrane is composed of cells, and increases by the formation of new cells. While the germinal membrane, in the direction of its superficies, separates into a central transparent and a peripheral opaque portion or area, it also undergoes a division in the direction of its thickness; for it is soon found to be composed of two layers, which, though not actually separate, yet have a different structure. The superior or external layer, which lies next to the vitelline membrane or proper membrane of the yolk-sac, is called the "serous layer;" the inferior or internal, in contact with the yolk itself, is named the "mucous layer." The structure of these two layers is as follows: — Schwann having folded the germinal membrane of an egg, which had been subjected during eight hours to the heat of incubation, in such a manner that its external surface was outwards, he found the folded margin, which of course was also formed by the external surface of the membrane, to be composed of extremely delicate transparent cells. These cells were of all sizes up to that of the globules which originally composed the germinal membrane before, and for a short time after, the commencement of incubation. They contained a transparent fluid and no nucleus; but in some there were seen a number of very small dark granules (fig. 185, A). In an ovum which had been subjected to sixteen hours' incubation, the mucous layer also was developed. The external surface at this period, according to Schwann, was formed of cells which had a nucleus attached to the inner surface of their wall with one or two nucleoli within the nucleus, and also a clear fluid with a few small granules (see fig. 185, B). These cells, owing to their being so closely pressed together, were polyhedral.* The internal

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* The most important works on this part of the subject of development are: C. Fr. Wolff's Theoria Generationis, Halæ, 1759; and his treatise, Ueber die Bildung des Darmcanals, übersetzt von Meckel, Halle, 1812; Pander's Entwickelungs-geschichte des Hühnchens im Ei, Würzburgh, 1837; Von Baer's additions to Burdach's Physiologie, Bd. ii.; and his Entwickelungs-geschichte der Thiere; Valentin's Entwickelungs-geschichte; and Wagner's Physiologie.

Fig. 184.

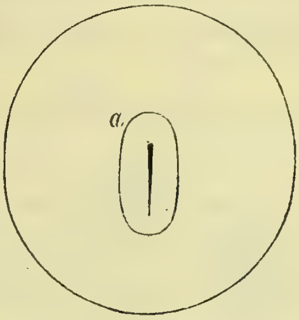
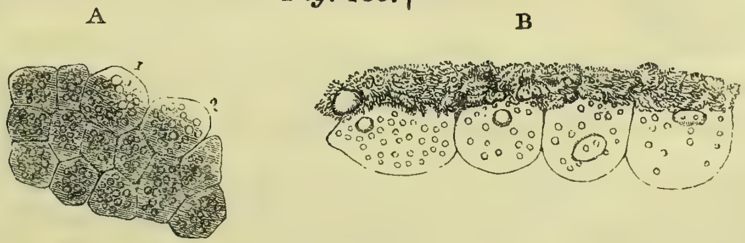


Fig. 185.†



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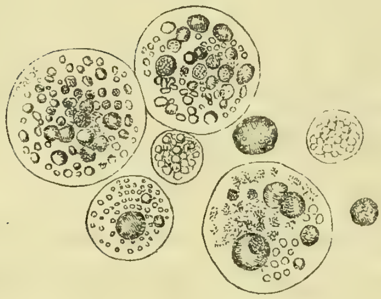
* Compare Valentin's observations, Entwickelungs-geschichte, p. 287.

† [Fig. 185, A, represents a portion of the germinal membrane of an unincubated egg. At the points 1 and 2, the cavity of the cells could be distinguished. B, a portion of the germinal membrane, after sixteen hours' incubation, folded so that the serous layer forms the lower border. After Schwann.]

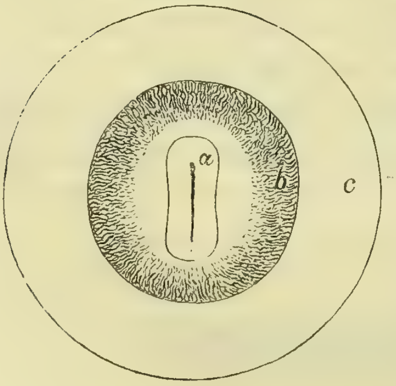
or mucous layer of the germinal membrane was formed, according to Schwann, of large cells which varied very much in size, and contained a transparent fluid and granules of different kinds. In almost every cell there was seen a globule distinguished by its dark circular outline, and sometimes there were several of these globules in one cell (see fig. 186). The cells of the mucous layer lie, not in very close contact with each other, in a structureless intercellular substance, their formative mass or "cytoblastema." This substance contains, besides the cells, a number of dark globules and smaller granules, a part of which are supposed by Schwann to be the nuclei of new cells. Within the area pellucida the cells of the mucous layer have a very different appearance. They are much smaller, and of pretty uniform size, very transparent, and containing, in place of a coarsely granular substance, only some very small globules. In these cells there is no nucleus; but the cells of the serous layer at the same part — the area pellucida—have a nucleus.

Fig. 186.*



The distinction between the area pellucida and the rest of the germinal membrane is not the only thing which presents itself for observation upon the surface of that membrane. Around the area pellucida two other distinct spaces soon become visible. These both have the form of a zone, and the boundary between them is a circle concentric with the margin of the germinal membrane. The space which lies within this circle, (*b*, in fig. 187,) and which is nearest to the transparent area (*a*), is called the "area vasculosa," because within it the blood-vessels form; and the space (*c*), which lies external to the same circle, is called the "area vitellina." This last zone extends itself more and more, and at a later period gradually encloses the whole yolk. The germinal membrane then becomes a closed sac containing the yolk, whilst the former vitelline membrane disappears.

Fig. 187.



The distinction between the area vasculosa and the area vitellina is produced by a change taking place in the substance of the germinal membrane. A new deposit is formed between the external and internal layer of the membrane. The blood-vessels are first developed in this deposit; and hence it has been named the vascular layer, although it cannot be easily isolated as a distinct layer. This third layer of the germinal membrane extends no further than the inner margin of the area vitellina; and hence the distinction which is produced between the area vasculosa and area vitellina,—a distinction which is perceived about the middle of the third day of incubation.

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* [Fig. 186 represents cells of the mucous layer of the germinal membrane, after Schwann.]

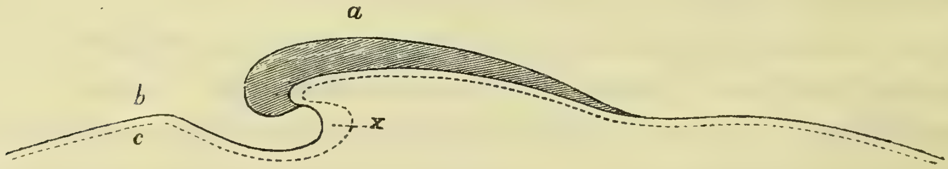
The first trace of the axis of the embryo becomes visible about this period in the form of a white streak, which occupies the middle line of the area pellucida. The long diameter of the transparent area is placed transversely to the axis of the egg, and this "primitive streak" has consequently the same position. The streak is thicker at its anterior or cephalic extremity, and tapers towards the opposite extremity. Von Baer regarded the primitive streak as the precursor of the vertebral column,—as a structure of only temporary persistence. To Reichert, on the contrary, it appeared to be no independent structure, but merely a groove. At the sides of this primitive streak, and parallel with it, two ridges or crests soon appear,—the "laminæ dorsales."

These ridges diverge slightly from one another, both anteriorly and posteriorly. According to the observations of previous embryologists, these parts are destined to embrace the rudimentary brain and spinal cord, by closing over them, being, in fact, the rudiments of the vertebral column and cranium. But Reichert maintains that they are themselves the lateral halves of the central nervous system. Beneath the spinal cord lies the "chorda dorsalis," a delicate gelatiniform thread, first discovered by Von Baer. This may be regarded as the axis of the bodies of the vertebræ and of the cranium, but it is not itself converted into the bodies of the vertebræ. For the "rudiments of the bodies of the vertebræ" appear as a double row of quadrangular white dense spots, symmetrically arranged at the sides of the chorda dorsalis. (See fig. 191, page 1538.) These rudiments of the vertebræ subsequently become prolonged into the arch and into the body, so that at length the axis of the bodies of the vertebræ, or the chorda dorsalis, in the chick, is found to be embraced from below by these soft structures. At first only a few of these rudimentary vertebræ exist, but they afterwards increase in number. Malpighi observed this development of the vertebræ from two lateral halves.

These rudiments of the axis of the embryo are closely connected on all sides with the external layer of the germinal membrane, and at first lie in the same plane with it. Subsequently the embryo, together with the immediately contiguous part of the germinal membrane, elevates itself above the level of the rest of that membrane in the form of a small boat (see fig. 189), enclosing a cavity open beneath, which is the first condition of the cavity of the trunk of the future animal. By the bending inwards of the germinal membrane anteriorly, posteriorly, and at the sides of the rudimentary embryo, this cavity becomes more and more cut off from the general cavity of the yolk-sac, and acquires inferior and lateral walls. The cephalic end of the embryo, with the anterior part of the body, first bends forwards and downwards, and the germinal membrane follows this depression of the cephalic extremity of the embryo. The fold of the germinal membrane, thus bent inwards, extends from before backwards, until the cephalic part of the embryo no longer forms part of the walls of the cavity of the trunk. (See fig. 188.)

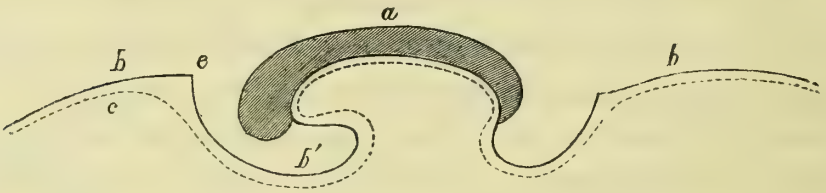
The portion of the germinal membrane thus bent or folded inwards is called the "involucrum capitis." It is to be observed as early as the first day of incubation, and appears first in the form of a transverse fold, which grows deeper and deeper. From the margin of this fold the peripheral part of the germinal membrane extends in its original direction.

Fig. 188.



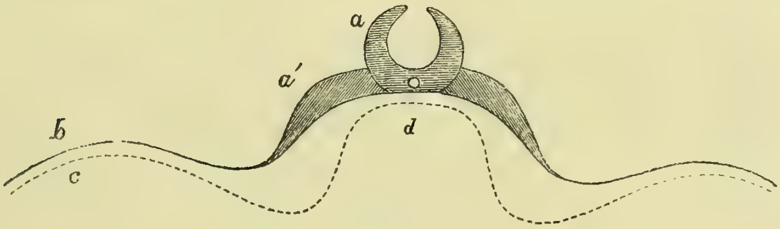
See figure 188, where *a* represents a longitudinal section of the embryo; *b*, the external layer of the germinal membrane, and *c*, the internal layer. During the second day of incubation a similar fold of the germinal membrane is formed at the caudal extremity of the embryo ("vagina caudæ"), and presses from behind forwards beneath it. (See fig. 189.)

Fig. 189.



These two folds are connected by that part of the boat-shaped embryo which passes off from the structures of the axis on each side into the expanded germinal membrane. In this way the embryo becomes in some measure separated by a constriction both anteriorly, posteriorly, and at the sides, from the rest of the germinal membrane above the surface of which it elevates itself, with the cavity of its trunk, still in great part open, turned towards the yolk. The part of the internal layer of the germinal membrane which lines the cavity of the embryo is the primitive form of the intestinal canal. That part of the external layer of the germinal membrane, on the contrary, which descends on each side from the rudimentary axis of the embryo, and contributes to its boat-like form, is continuous with the rudimentary structures which are destined to form the parietes of the trunk, namely, the walls of the neck, chest, and abdomen. (Rathke's observations, however, have shown that the animal structures forming these parietes of the body are not wholly developed from the external layer of the germinal membrane.) In a transverse section of the embryo at this stage (in fig. 190) the external layer of the germinal membrane is seen to be continuous with those structures which form superiorly the "dorsal laminæ," the future envelope of the spinal cord, and inferiorly the "abdominal or visceral laminæ," destined to enclose the visceral system.

Fig. 190.



In fig. 190, *a* represents the dorsal portion, and *a′* the abdominal portion of the animal parietes of the cavities of the trunk; *b*, the peripheral part of the germinal membrane; *c*, the internal layer of the germinal membrane; and *d*, the organic part of the embryo,—the primitive form of the intestinal or digestive system.

The changes in the middle layer of the germinal membrane within the vascular area have in the mean time laid the foundation for the development of the "vascular system" and "the blood." At the circumference of the vascular area insulated spots and canals make their appearance, and these soon unite so as to form a network filled with a pale yellow transparent fluid. About the same time the "heart" is formed in the same layer of the germinal membrane, and at that part of it which is reflected downwards from the cephalic portion of the embryo, so as to enclose the anterior part of the cavity of the body. (See fig. 188, in which the letter *x* indicates the situation of the heart.) According to Schwann's observations, the blood-vessels are developed originally from nucleated cells. These cells, he states, send out processes; the processes from different cells unite; and in this way ramifications and a network are produced. Vessels extend from this network in the area vasculosa into the area pellucida, and join the rudimentary heart. The heart itself has the form of a long tube, which is prolonged inferiorly into two venous trunks, and superiorly into several "aortic arches," (at least three in number,) on each side. These aortic arches unite beneath the vertebral column, and form the "aorta." (See fig. 191.) The vascular layer now ramifies in the animal, as well as in the organic system of the embryo, and aids essentially in its further development. Some of the vessels or canals forming the network become enlarged into trunks,

Fig. 191.*

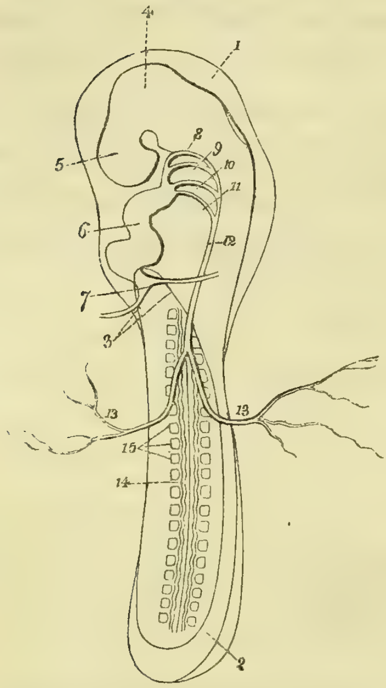
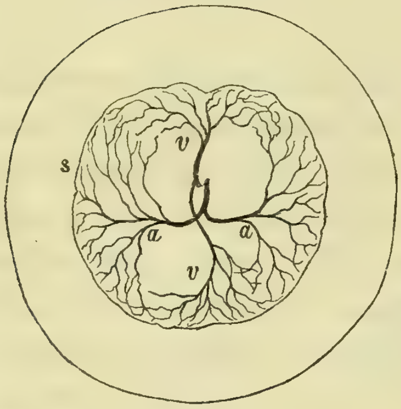


Fig. 192.



and when the heart begins to pulsate, a fluid circulates, which is at first colourless. Red "blood corpuscules," however, soon form in the area vasculosa. These corpuscules are at first globular, but at a later period they assume the elliptic form which characterises them in the adult bird. According to the observation of Schultz,† the nuclei appear first, and the red envelope subsequently. The primitive form of the embryonic circulation is as follows. The aorta divides into a right and a left branch, and these are continued as the "arteriæ omphalo-meseraicæ," (*a*, *a*, fig. 192,) into the germinal membrane, where they ramify and anastomose until they reach a circular venous canal (*s*) which surrounds the area vasculosa. From this venous canal, the "sinus terminalis," and from the vascular network of the germinal membrane, the blood is brought back by the "venæ omphalo-meseraicæ," (*v*, *v*,) which issue from the area vasculosa at points corresponding to the anterior and posterior extremities of the embryo. Subsequently other veins are developed in the vascular network, which follow the course of the arteries; and at length, when the germinal membrane has enclosed the whole yolk, the terminal sinus entirely disappears, and the whole yolk-sac becomes covered with blood-vessels.

In the course of the third day of incubation the "amnion" is developed. It is formed by the external layer of the germinal membrane, which rises in the form of a fold around the embryo. This fold first becomes visible when the germinal membrane is drawn down to form the body of the

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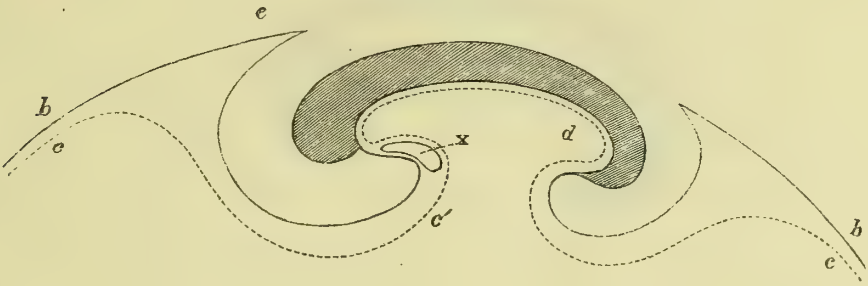
[*] [Embryo of the chick at the commencement of the third day, as seen from the abdominal aspect, and magnified. After Wagner. Icones Physiol. Tab. iv. 1. The involucrum capitis; 2. the involucrum, or vagina caudæ; 3. passage of the involucrum capitis into the lateral folds of the germinal membrane; 4. prominence of the corpora quadrigemina or optic lobes of the brain; 5. the anterior cerebral mass or hemispheres; 6. the heart; 7. entrance of the great venous trunks in the atrium cordis or auricle; 8, 9, 10, and 11. the four aortic arches; 12. the descending aorta; 13. the arteries of the germinal membrane; 14. the dorsal laminæ, rendered slightly wavy by the action of water; 15. the rudiments of the vertebræ.]

[†] System der Circulation.

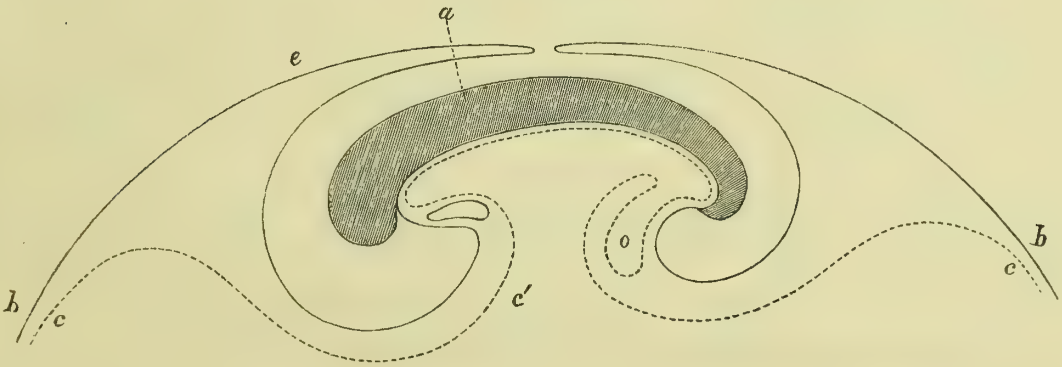
embryo (see fig. 189, page 1536). It forms a sort of hood over the cephalic end of the embryo, and then is reflected back in its original course.

Fig. 193.



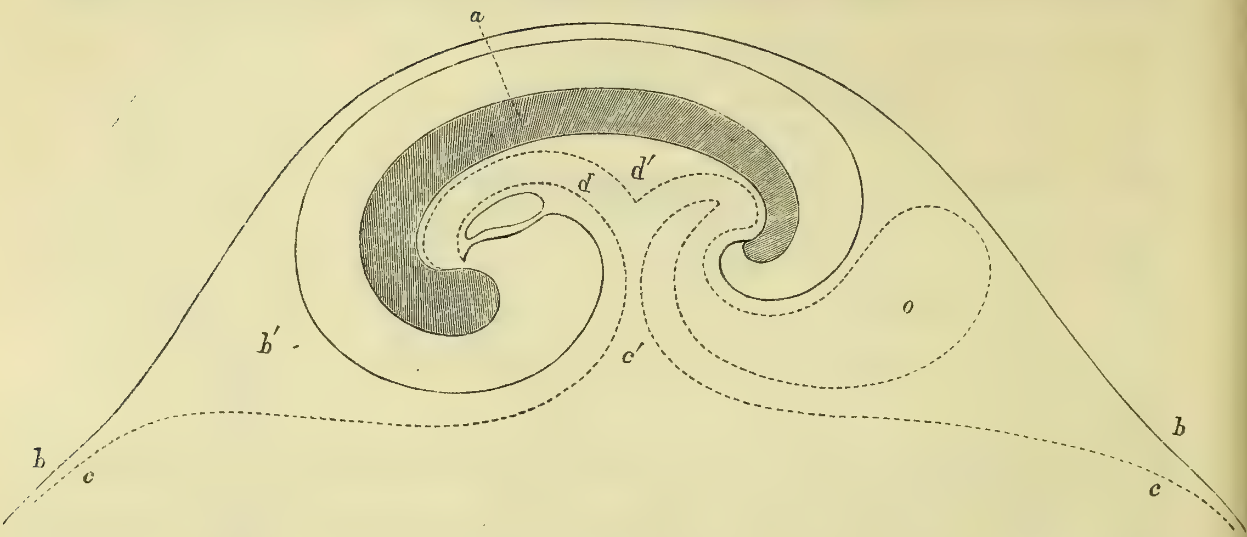
In fig. 193 this fold has increased; *b* and *c* here indicate the outer and inner layers of the germinal membrane; *d*, the cavity of the organic system of the embryo; and *c′*, the point of union of this system with the internal layer of the germinal membrane. From the external layer of the germinal membrane, *b*, a fold, *e*, is seen rising, and separating itself from the inner layer. This fold extends more and more over the cephalic portion of the embryo (see fig. 194, *c*), forming a complete sheath for it.

Fig. 194.



A similar fold rises from the same layer of the germinal membrane at the caudal end of the embryo, over which it extends, so as to form a similar sheath for it. (See figs. 193 and 194.) And a similar fold is formed at each side. These folds are all continuous, and, as they extend over the body of the embryo from its abdominal towards its dorsal aspect, they at length meet there and coalesce. (Fig. 195.) The embryo then lies completely enclosed in a non-vascular shut sac, the amnion, which contains a fluid, the "liquor amnios." The upper or external layer of the fold which produces the amnion is at this part of the ovum separated from the yolk and from the internal layer of the germinal membrane, with which it elsewhere lies in close contact, by the embryo. The true amnion formed by the inner lamella of the fold now constitutes a shut sac, which is continuous with the skin of the embryo at the former line of union of the parietes of its body with the external layer of the ger-

Fig. 195.



minal membrane. The parietes of the body of the embryo are therefore reflected upon themselves, as it were, so as to form the membrane of the amnion. The part at which the reflection takes place is the umbilicus. This at first is wide and long, but it gradually grows smaller. The inner layer of the germinal membrane remains continuous with the intestinal cavity. The constricted part at which the inner layer of the germinal membrane is continued into the wall of the intestinal cavity or tube (fig. 195, *c′*), is now called the vitelline duct, ductus vitello-intestinalis; the inner layer of the germinal membrane having at this period extended over the whole yolk, and become the vitelline sac. The communication between the yolk-sac and the intestines was pointed out by Stenonis; but it had previously been observed by Fabricius in the chick, after its escape from the egg. The vitelline duct passes through the umbilical opening; it is at first wide, but gradually diminishes in size.

The liver, as was first discovered by Rolando, is formed by the protrusion of a part of the primitive walls of the intestine. Von Baer observed the same fact, and their statements are confirmed by my own observations. For although I could not discover the protrusion of the walls of the intestinal tube in the Bufo obstetricans, either because I sought it at the wrong time, or because it does not take place in that animal, yet I saw it distinctly in the chick on the fourth day of incubation.* Valentin also has confirmed the accuracy of Rolando's observation. It is therefore very remarkable that neither the liver nor the lungs, which, according to Rathke, are developed by the same process, appeared to Reichert to be formed by protrusion of the intestinal walls.

Before the close of the third day the allantois also is formed (indicated in figs. 194 and 195 by the letter *o*). It is developed, according to the observations of preceding embryologists, by the protrusion of a part of the walls of the terminal portion of the intestine. But it appeared to Reichert to be merely connected with the excretory ducts of the corpora Wolffiana, or primordial kidneys,—organs of which we shall treat in a future chapter. The allantois is an elongated vascular sacculus, which protrudes through the umbilicus, and increases in size until it becomes a large vascular sac. The pedicle of this sac is the urachus which passes with the ductus vitello-intestinalis through the umbilicus, and is accompanied by the vasa umbilicalia, just as that duct is by the omphalo-mesenteric vessels. The allantois increases to such a size as to envelope the embryo, together with the amnion and yolk-sac. The vascular net-work which covers it serves the purpose of respiration.* The blood-vessels of the embryo will be described in the succeeding section.

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* Müller. De Glandul. struct. penit. Tab. x.

While the development of the embryo proceeds, and the structure and tissues of the different organs are perfected, the vitelline or yolk-sac gradually diminishes in size. At a later period it is received wholly within the abdominal cavity, and there remains connected with the intestine by the vitelline duct, while the umbilicus closes. The yolk-sac is still to be found within the abdominal cavity in birds and reptiles which have escaped from the shell. In fig. 196, *a* represents the dorsal structures of the embryo; *b*, the amnion; *c*, the yolk-sac; *c′*, the vitelline duct; *o*, the allantois; and *o′*, the urachus.

The development of crocodiles, serpents, lizards, turtles, and tortoises, seems to conform to the same general principles as those which regulate the process in birds. They all have a yolk-sac, which is origin-

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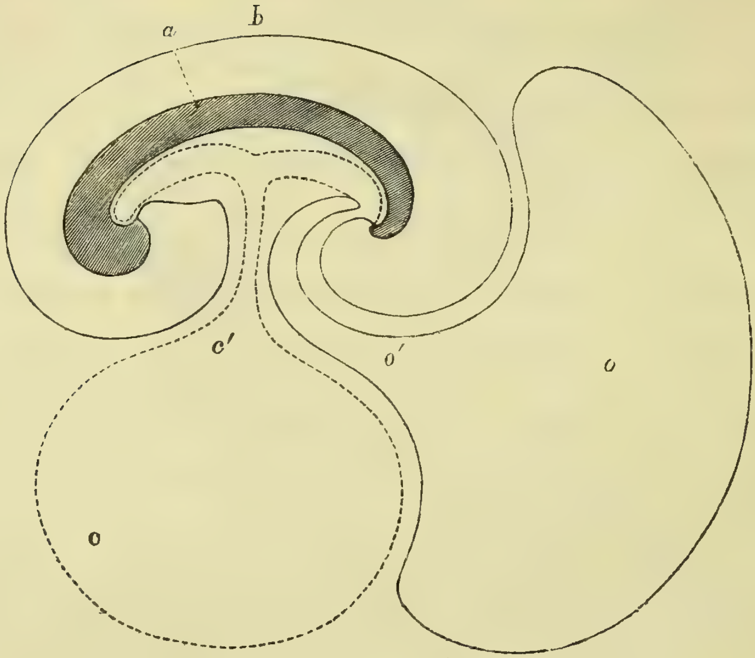
* [Mr. Dalrymple, who has succeeded in making some very perfect injections of the allantois of the chick, has most kindly furnished the following account of the vessels of that membrane:—

“ The allantois of the chick has a double order of vessels, which in some sort divides it into two proper membranes, artificially separable from each other. On the outer surface (that next the memb. testis) the larger arteries and veins ramify and inosculate under repeated angles, while on the inner surface is arranged a uniform layer of minute capillaries, constituting a most beautiful and regular system of pulmonary vessels. When this membrane has been minutely and thoroughly filled by injection, it presents an equally red surface that, viewed under a compound microscope with a half-inch object glass, shows the capillary vessels to be uniform as to size throughout, and so densely arranged, and so repeatedly anastomosing with each other, that the rhomboidal areas between them do not even equal the diameters of the vessels. The regularity of these spaces, both as to size and shape, their close approximation, and the minuteness of the capillaries themselves, indicate the extreme subdivision of the blood-vessels of this membrane, and resemble in a strikingly exact manner the vesicular lungs of the Batrachian and Saurian tribes. The arrangement of the vessels at the bottom of the pulmonary cells of the frog, with the single exception of the larger size of the capillaries, presents so complete a similitude as to justify us in considering the type of the distribution of the vessels of the allantois to be strictly pulmonary, and is a further confirmation of the so much disputed respiratory function of this membrane in the bird.—J. D.”]

Fig. 196.



ally connected with the intestine; but in serpents, according to the observations of Volkmann and Rathke, this connection ceases to exist at an early period. They have an amnion and an allantois.* All reptiles, however, are characterised by the presence of numerous looped and anastomosing vessels hanging from the inner surface of the membrane of the vitelline sac into the yolk. These are a further development of those convoluted vessels (the vasa lutea), which present themselves on the inner surface of the yolk-sac in the egg of the bird.†

2. *Development of the different systems of organs in the ovum of the bird.*‡

The cells of the germ-disk and those of the yolk-cavity alone contribute directly to the formation of the embryo. The cells of the substance of the yolk, on the contrary, appear at no period to aid directly in the formation of the embryonic structures. The nucleus of the cicatricula, or cumulus germinativus, which is to be regarded as merely the most superficial stratum of the cells of the yolk-cavity, accumulated in the canal leading from that cavity to the germinal disk, cannot be entirely isolated from the disk either in a mature unimpregnated egg or in an egg in which development is commencing. When the first rudiments of the embryo are formed, the nucleus cicatriculæ is set free, and soon entirely disappears.

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* See Emmert and Hochstetter, über die Entwickelung der Eidechsen. Reid's Archiv. x. p. 84; Tiedemann über das Ei der Schildkröten. Heidelb. 1828; Volkmann, De colubri natricis generatione. Lips. 1834; Rathke, Entwickelungs-geschichte der Natter, Königsberg, 1839.

† [See the description of the yolk-sac and vasa lutea of the chick by Mr. Grainger, at the end of this chapter.]

‡ From Reichert's manuscript communication.

During the first epoch of the process of development all the structures of the embryo are formed by the direct apposition, in successive strata, first of the cells composing the germinal disk, and subsequently of the neighbouring cells of the yolk-cavity ; the rudimentary structures thus formed being enlarged by the addition of new cells of similar kind. No nutritive material is yet conveyed to these cells in any way. They increase, for the purpose of giving the individual structure to the different rudimentary organs, at the expense of the abundant globular matter contained within them. This matter gradually disappears, while numerous young cells appear in some of the embryonic structures.

" *Investing membrane*."—The first step preparatory to the development of the new organism from the ovum is in the chick, just as in the frog, the formation of an investing membrane, under the protection and by the aid of which the subsequent vital changes attendant on the development of the embryo proceed. This first product is seen upon the surface of the cicatricula or germ of every impregnated egg as soon as it is laid. It has the form of a circular disk, of the same size as the cicatricula itself. It is the first stratum of cells which assumes a distinctly membranous form upon the surface of the cicatricula, but it cannot, during the first few hours of incubation be in any way separated artificially as a continuous membrane. Its presence is evinced by the distinctly circumscribed outline which it gives to the germ-disk, and is recognised under the microscope by the polyhedral cells of which it is composed. This new structure has hitherto been called the serous layer of the germinal membrane; but it has precisely the same functions as the dark " investing membrane" of the frog's ovum (see page 1521). It consists at this period, as Schwann has described it, under the name of the germinal membrane, (see page 1515,) of closely aggregated cells of various sizes, with a dark aspect, and globular contents. At first these cells have no visible membranous wall and no nucleus. The growth of this investing membrane advances constantly ; with its centre fixed at the place of development of the embryo, it extends uniformly at its circumference between the yolk and the vitellary membrane. The first extension of the membrane takes place by the expansion of the cells originally composing it, these cells acquiring at the same time greater transparency, and their membranous wall becoming visible. Subsequently the investing membrane grows by the apposition of new cells of the yolk-cavity to its periphery, while a finely globular deposit takes place upon the nucleus of these cells, and renders them similar to the cells of the germinal disk. The " investing membrane " is one of those structures of the embryo which are entirely formed by the aggregation of the cells of the yolk-cavity, without any aid of the vascular system.

Primitive rudiments or foundation of the central nervous system.—The development from the yolk of those structures which belong entirely and peculiarly to the embryo, commences by the formation of the central organs of the nervous system. In the frog, the formation of these organs does not begin until the investing membrane has extended over the entire surface of the yolk; but in the chick, that membrane has reached only a few lines beyond the circumference of the germ-disk or cicatricula, before the commencing development of the structures proper to the embryo is evidenced, by the appearance of a whitish streak which traverses the centre of the circular disk, dividing it into two equal parts, without, however, reaching its circumference at either extremity. This primitive streak is the reflection of a shallow groove, resulting from the formation of the lateral halves of the central nervous system on each side of the line which it occupies. Shortly afterwards the chorda dorsalis, distinguished by its white colour, is found running beneath the groove in its whole length; but the lighter colour of the groove is not due to the presence of this chorda dorsalis beneath it, for it disappears when the groove is obliterated by traction on each side, while similar white streaks may be produced by forming artificial grooves or furrows, at any part of the investing membrane. The natural form of the primitive groove may be seen very distinctly in transverse sections of the investing membrane. The rudiment of the central nervous system lies immediately around the primitive groove attached to the under surface of the investing membrane. Just as in the frog, it is formed of a membrane-like stratum of cells, which has separated itself from the germinal mass. When these parts are examined beneath the microscope, the cells of the "investing membrane," which have already become more transparent, and present a distinct membranous wall and sometimes a nucleus, are seen first, and beneath them the newly deposited cells of the rudimentary nervous system, as yet quite filled with globular contents. The primitive lateral halves of the nervous centres in their earliest condition have the form of two membrane-like layers of cells, deposited upon the under surface of the "investing membrane," at each side of the primitive groove, and uniting with one another before and behind, so as to form together an oval surface, which is traversed in the longitudinal direction by the primitive groove.

Membrana intermedia.—So soon as the layer of cells destined to form the rudimentary nervous centres has become isolated from the surface of the germinal disk, the second mass of cells destined to the formation of the structures of the embryo separates from the surface of the germ-disk, in the form of a pretty firm consistent membrane, of circular outline, and thicker than the strata of cells which previously separated themselves. This membrane, at first, nearly equals in extent the investing membrane, with which its upper or external surface is in close relation at its periphery, while at its centre it lies in contact with the rudimentary nervous centres. It extends beyond the limits of the area pellucida or germinativa. It is often possible to isolate this membrane, except at the point where it is in contact with the chorda dorsalis.

The membrana intermedia is of the greatest importance in the development of the higher vertebrata. Earlier observers have probably regarded it at first as the mucous layer of the germinal membrane, and subsequently as the vascular layer. It lies between the rudimentary nervous centres and the mucous membrane, which is soon afterwards formed. It is the common rudimentary mass from which are developed the vertebral, cutaneous, and sanguineous systems, and the intestinal or digestive system, with the exception of the mucous membrane; and it is the active medium of reaction or communication between the yolk and the rudimentary structures of the embryo which at this period exist, and which are merely the central nervous system and the mucous membrane.

The inferior tube or visceral cavity of the embryo is produced by the following process. Hitherto the central nervous system and the membrana intermedia formed a nearly plain surface, the only interruptions to which were the very slight convexities of the lateral halves of the nervous centres and the groove lying between them. These convexities, however, now increase, forming the parts hitherto designated the dorsal plates, and at length produce the superior vertebral tube, which is developed above the level of the surrounding part of the embryo and ovum. The inferior surface of the embryo, as yet plane, is formed by the membrana intermedia. This membrane now becomes bent downwards and backwards at a short distance in front of the central nervous system, and in a line corresponding to the almost semicircular outline of its cephalic extremity; whilst from the most posterior margin of this inflected part, the membrane again passes forwards and becomes continuous with its peripheral portion. This second returning part of the fold is the involucrum capitis of Von Baer. By this bending inwards of the membrana intermedia the anterior part of the embryo comes to enclose a hood-like cavity, which opens into the yolk-cavity, and which afterwards becomes the visceral cavity of the head and neck, with the structures belonging to those regions. The opening into this hood-cavity is not in the place of the anterior orifice of the future digestive canal, but corresponds nearly to the situation where the stomach is afterwards placed. The mouth is developed at a later period, more anteriorly in the closed wall of the hood. The original opening into the hood-like cavity was not unaptly named by Wolff the *fovea cardiaca*.

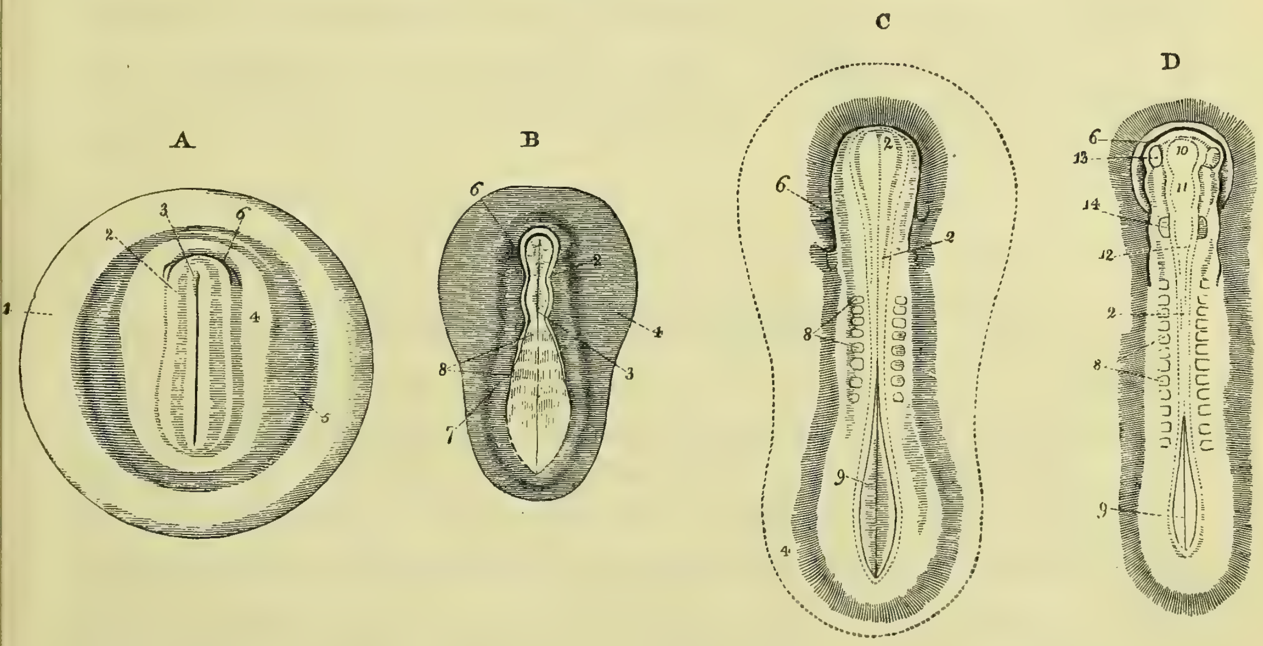
Development of the mucous membrane.—When the cephalic portion of the visceral tube of the embryo is formed, the last membranous layer of cells separates from the germinal disk, and forms the rudiment of the intestinal mucous membrane, at the under surface of the membrana intermedia. The rudiment of the mucous membrane is circular, like the germinal disk, and does not extend quite so far in circumference as the membrana intermedia. The latter membrane, as well as the "investing membrane" beyond it, is covered internally by a layer of the cells of the yolk-cavity which has extended from the circumference of the cumulus germinativus. This layer of cells, of white colour, appears to be directly continuous with the rudimentary mucous membrane; but differs from it both in function and elementary structure. The rudimentary mucous membrane is at this period composed of the same "cells of the yolk-cavity," filled with finely globular contents, which form the other structures of the embryo in their earliest condition. This layer of cells, composing the rudimentary mucous membrane, is not, however, at all points applied closely to the under surface of the membrana intermedia. On the contrary, that part of the membrana intermedia, which encloses the hood-like cephalic portion of the visceral cavity of the embryo, is withdrawn from immediate contact with the mucous membrane. For the latter membrane passes in a plain direction across the posterior opening into the hood. However, when the hood enlarges anteriorly this septum stretched, as it were, across the opening, does not expand at the same time; but becomes atrophied or absorbed, so that an opening is formed in the mucous membrane, corresponding to the orifice of the cephalic visceral cavity. The part of the visceral cavity just named, is therefore developed independently of the mucous membrane; and the opening through this membrane forms the future œsophageal orifice of the stomach, where the central organ of assimilation commences.

When the rudiment of the mucous membrane is formed, the proper function of the germinal disk in the process of the development of the embryo ceases. Being a round disk, composed of the accumulated formative cells of the yolk-cavity, it was, up to this period, well fitted to form the membranous rudimentary structures of the embryo, by the separation of successive strata from its surface; but in the further development of the embryo it serves no purpose. It is true, there is seen for some time, beneath the embryo, a whitish mass of cells. This is the nucleus of the cicatricula, or the cumulus germinativus of earlier embryologists, which has become isolated, as it is said, from the rudimentary embryo. This mass of cells, however, consists only of the ordinary cells of the yolk-cavity, which have, for the most part, suffered no great internal changes; and it has no special connection with the embryo itself. It represents merely the cells of the yolk-cavity in the canal leading from that cavity to the germ-disk, these cells appearing white owing to their close aggregation, though in respect of the development of the embryo they have no greater importance than the other cells of the yolk-cavity.

During the development of the different rudimentary structures of the embryo just described, not only is the membranous wall of the cells observed to become manifest at the expense of the globular matter contained within them, but young cells are seen to be developed within parent cells.

The membranous lateral halves of the rudimentary nervous system now manifest a tendency to contract towards the middle line, and to unite, while the future envelopes of the nervous centres, developed from the membrana intermedia, rise simultaneously with them. When the union of the lateral halves of the nervous centres commences, their oval form undergoes a change; for a lateral indentation presents itself about the middle of their length. This is the first indication of the future distinction between the brain and spinal cord. (See fig. 197, A & B.) The process of union of the two lateral halves commences in the chick at the brain and extends gradually to the spinal cord (fig. 197, B & C). During the contraction of the rudimentary nervous centres towards the median

Fig. 197.*

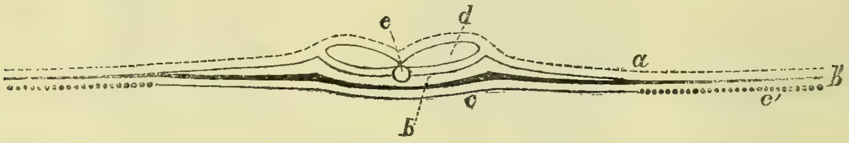


* [Fig. 197 represents the earliest stages in the development of the embryo, and more especially of the rudimentary nervous centres of the embryo of the common fowl. After Reichert. In all the views, 1, indicates the "investing membrane;" 2. the rudimentary nervous centres; 3, the primitive streak or groove; 4, the pear-shaped internal portion of the "membrana intermedia," which corresponds also to the "area pellucida;" 5, the peripheral portion of the membrana intermedia, which corresponds to the "area vasculosa;" 6, the fold which passes backwards and insulates the cephalic portion of the "membrana intermedia" and the head of the embryo; 7, the commencing cutaneous system; 8, the rudiments of the vertebræ, (in fig. B, still covered by the rudimentary nervous centres;) 9, part of the dorsal furrow not yet converted into

line, they increase somewhat in thickness ; supported by their rudimentary envelopes which are rising beneath them, they elevate themselves by their outer margins and convert the primitive groove into a furrow, bounded by two ridges. Over this furrow lies the " investing membrane," and beneath are perceived the rudiments of the vertebra. The union of the lateral halves of the nervous centres consist in the coalescence of the outer margins of this furrow, which takes place first at the brain, and which, when completed, converts the central nervous system into a complete tube.

Central and peripheral parts of the membranous rudimentary structures of the embryo.—In the membrana intermedia a central and a peripheral portion are to be distinguished. The central portion has anteriorly formed the cephalic part of the visceral cavity ; the peripheral portion continues in its original course beneath the investing membrane. This peripheral portion of the membrana intermedia forms a zone, corresponding to the circuit of the future area vasculosa. Beneath the central portion lies the mucous membrane, the peripheral prolongation of which is the cortical layer of the yolk. Near the embryo this cortical layer of the yolk lies in contact with the under surface of the peripheral portion of the membrana intermedia, but beyond this, at the inner surface of the " investing membrane." In the situation of the embryo itself, therefore, we find four strata arranged in the following order, taking them from without, inwards :—First, the investing membrane indicated in the section, fig. 198, by the letter *a ;* next, the central nervous system (*d*)*;* next, the central portion of the membrana intermedia (*b*), with the chorda dorsalis (*e*)*;* and most internally, the mucous membrane (*c*). More externally, in the circumference of the embryo, there are three layers, of which the most external is the investing membrane (*a*)*;* the middle one, the peripheral portion of the membrana inter-

Fig. 198.



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a closed canal by the arching over of the rudimentary lateral halves of the nervous centres ; 10, the most anterior division of the brain, the vesicle of the third ventricle; 11, the second division of the brain, the vesicle of the aqueductus Sylvii ; 12, the third division of the brain, or vesicle of the fourth ventricle ; 13, rudiment of the optic nerve ; 14, rudiment of the auditory nerve. In A, the lateral halves of the nervous centres are in their first and simplest condition ; in B, their outer margins are becoming elevated ; in C, the outer margins of the opposite halves have united in a great extent, converting the former groove into a canal ; and in D, the three primary divisions of the brain are visible, and the rudiments of the higher organs of sense are formed.]

media (b'), and the most internal, the cortical stratum of the yolk (c'), which is continuous with the mucous membrane (c). At a still greater distance from the embryo, and thence over the whole surface of the yolk, that is to say, from the margin of the membrane intermedia, only two layers are to be found,—first, the investing membrane (a) and the cortical stratum of the yolk (c'). The cortical layer of the yolk, together with its central part, the rudimentary mucous membrane, constitutes what was termed the mucous layer of the germinal membrane by former embryologists. The cortical layer is composed of cells of the yolk-cavity, both in their simple form and in different states of metamorphosis. The nearer these cells are to the area vasculosa, the more advanced are these metamorphoses of development. Several lines from the area vasculosa there is a circle, in which the cortical layers of cells is distinguished by greater opacity and a whiter colour, and here a part of the cells have developed young cells in their interior. This state exists in a still greater degree beneath the area vasculosa. At the line of transition of the area vasculosa to the area pellucida, the cortical layer of the yolk is more transparent, and the cells composing it contain merely globules. It here is in relation with the cells of the mucous membrane.

Changes of development which take place in the membrana intermedia up to the formation of the sanguineous system.—In all the further stages of development of the embryo, the membrana intermedia plays the most important part. The great difference between the development of the ovum of the frog and that of the bird may in some measure be reconciled, by supposing that here the membrana intermedia takes the place of the vegetative and formative yolk of the former animal. Thus the central portion of the membrana intermedia gradually developes from its surface, (at first by its own vegetative power, and afterwards with the aid of the sanguineous system,) the auxiliary system of the central organ of animal life, and then the sanguineous system itself, and lastly, after being pushed more and more downwards and inwards, becomes the intestinal system, which forms the support of the central organ of vegetative life, namely, the mucous membrane. The first products of the development of the centre of the membrana intermedia, without the aid of the sanguineous system, are the rudiments of the cutaneous system, and of the vertebral plates, and the formation of the sanguineous system which is essential to the further development of the embryo.

The rudiments of the cutaneous system and of the primitive plates of the vertebral system are formed nearly simultaneously at the period when the lateral halves of the central nervous system begin to contract towards each other for the purpose of uniting, and to elevate themselves from the level of the surrounding surface. The primitive plates of the vertebral system have then separated themselves as membranous laminæ from the membrana intermedia on each side of the chorda dorsalis, and are in their whole extent covered by the rudimentary nervous system, with which they correspond in length and breadth. The existence of the vertebral plates is evinced with the greatest certainty by the appearance of some of the segments of the vertebræ. The rudiments of the cutaneous system appear at each side of the vertebral plates upon the contiguous surface of the central portion of the membrana intermedia. The presence of the cutaneous system is rendered certain by the development of the membrana reuniens superior and inferior, which immediately follows. In proportion as the development of the cutaneous system proceeds, a new formation takes place in the membrana intermedia, corresponding to the growth of the visceral plates.

The rudiments of the vertebral and cutaneous systems form first the envelopes for the central nervous system; namely, the laminæ dorsales and the membrana reuniens superior. The walls of the visceral cavity are not produced until a later period, when the viscera themselves are developed. The sanguiniferous or vascular system manifests itself in the area pellucida or germinativa, by the formation first of the tubular part and afterwards of vessels. The situation where the heart is developed is the middle of the posterior margin of that fold, by the inflection of which the cephalic portion of the visceral cavity was formed. The mass of cells which constitute the rudimentary heart was separated from the under and inner surface of the membrana intermedia. The heart itself has the form of a cylinder, from both of whose extremities two branches are given off. The anterior branches lie in the side-walls of the cephalic visceral cavity, and there arch forwards and upwards towards the under surface of the vertebral tube. These are the rudiments of the first aortic arches. The branches given off from the posterior extremity of the tubular heart turn towards the free border of the fold, and then run outwards to the area vasculosa, which occupies the peripheral portion of the membrana intermedia. These are the main venous trunks. The vessels as well as the heart are at first composed of free cells loosely aggregated together, and have then no cavity. By degrees their external surface becomes more solid, and the heart, which has assumed a sigmoid flexure, begins its contractions with a very slow rhythm. The cells lying loose in its cavity are by these contractions expelled into the first aortic arches, whilst new cells enter from the interior of the main venous trunks. The first blood-cells differ in no respect from the delicate cells which compose the different tissues: they are round, and have a nucleus with a finely granular aspect and nucleoli. Their cell-cavity contains minute granules.

While the central part of the vascular system, with blood-cells, is formed in the area germinativa, a development of young cells within parent cells takes place in the peripheral part of the membrana intermedia which occupies the area vasculosa. Before the appearance of the bloody points in the area vasculosa, its peripheral part viewed with a magnifying power of 450 diameters, is seen to be composed merely of delicate cells uniformly disposed and separated by no intercellular substance. When the contractions of the heart commence, the blood-dots soon show themselves, and the peripheral part of the membrana intermedia presents under the microscope an irregular accumulation and distribution of the cells. Between the darker, irregular spots of the membrane, lighter parts are seen in which the cells are arranged singly side by side, and have acquired an increased thickness of their wall, as if for the purpose of forming a membrane. By the time that vascular canals can be distinguished in the area vasculosa, the brighter parts have acquired a very transparent aspect; nuclei of cells can be distinguished here and there; but the walls of the cells have so completely coalesced, that the outlines of the distinct cells can no longer be distinguished. At the same time the darker and more irregular masses of cells are perceived to have become sanguineous canals filled with blood-cells—the veins of the area vasculosa. About this period the smallest of the vascular canals always contain several blood-cells arranged side by side. Besides these venous trunks other canals are seen in the area vasculosa, running between the peripheral part of the membrana intermedia and the subjacent cortical stratum of the yolk. The walls of these canals are chiefly formed by the cells of this stratum of the yolk; these are the vitelline arteries. It is probable that the young cells produced within the yolk-cells form the blood-cells or corpuscules. The fully-formed cells of the yolk-cavity are, however, four or five times larger than the blood-cells, which certainly are not formed directly from these so-called yolk granules.

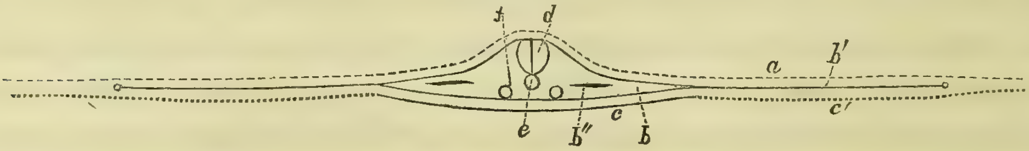
The aorta runs between the primitive laminæ of the vertebral system and the rest of the membrana intermedia, and soon divides into its two main branches. A short distance below the point of division these branches give off the vitelline arteries (arteriæ omphalo-mesentericæ).

The rudimentary mucous membrane receives no blood-vessels. The cells composing it increase in number by the development of young cells; but this process takes place slowly. The globules forming the contents of these cells are gradually converted into a transparent fluid, and young nuclei are formed which develope small cells, and at length are converted into the cone-shaped cells of the mucous membrane of the perfect animal. After the closing of the superior vertebral tube by the membrana reuniens superior, a tendency to form the membrana reuniens inferior becomes manifest.

Amnion.—The Amnion is a part developed from the membrana reuniens inferior. It appears originally at the border of the involucrum capitis, where the inflected membranes again assume their original direction in their peripheral portion. It is not, however, formed by the rising of a fold of the serous layer of former writers (our "investing membrane"), but by a special lamina (B, fig. 200) separated from the membrana intermedia, which is merely invested by a fold of the "investing membrane." This new lamina rises so as at length to arch over the head of the embryo. In the mean time laminæ destined to form the amnion have separated from the membrana intermedia in the whole circumference of the abdominal portion of the superior vertebral tube. They meet at the posterior extremity and there form the caudal sheath. Thus in the whole circumference of the embryo a lamina derived from the cutaneous system bends upwards, over the back of the embryo, its reflection taking place at that part where it seems to be about to form the boundary of the abdominal cavity. The coalescence of these laminæ above the dorsal region converts the amnion into a closed sac.

Figures 199, 200, and 201, represent transverse perpendicular sections of the embryo. In fig. 199, *a* indicates the "investing membrane;"

Fig. 199.



b, the membrana intermedia; *b'*, the peripheral part of that membrane; *c*, the mucous membrane; *c'*, its peripheral portion; *d*, the central nervous system; *e*, the chorda dorsalis; *f*, the two branches of the aorta; *b''* the line showing the commencing separation of the lamellæ of the amnion from the membrana intermedia. In figs. 200 and 201, the separation of the laminæ of the amnion is seen to become complete; and B indicates the membrana reuniens inferior, or lamina of the amnion, which in fig. 201 is turning upwards to form the amnion.

Fig. 200.

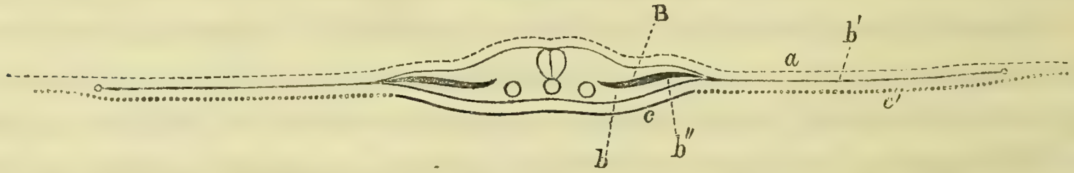
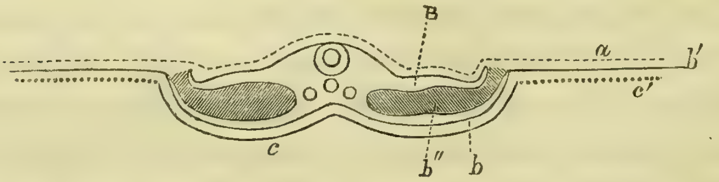


Fig. 201.



While the laminæ of the amnion are extending inwards to coalesce, the "investing membrane" forms a fold about their edge, and when they unite it is divided, just as happens when the two halves of the rudimentary nervous system coalesce by their upper edge (see figs. 202 and 203). The part which remains external to the amnion, and the continuity of which is again restored, forms the so-named serous tunic which retains the essential function of the investing membrane. The part included within the cavity of the amnion is still to be found there for a certain time, but it at length entirely disappears. The detachment of the laminæ of the amnion extends inwards to about the point where the great vascular trunks run between the rudimentary vertebral system, and the rest of the membrana intermedia. Here the connection between the animal system and the other structures not yet developed, but which are represented by the membrana intermedia, is still maintained. (See figs. 200 to 203.)

When the brain has become drawn down in nearly half its extent over the cephalic portion of the visceral cavity or tube, the visceral or abdominal laminæ begin to develope themselves, and to extend downwards from the same part of the rudimentary vertebral system from which the superior dorsal laminæ take their rise. At the cephalic part of the embryo they appear as the visceral processes (the so-named branchial arches), which extend downwards, and gradually unite to form the three visceral arches.

After the development of these arches, and of the three aortic arches connected with them, the brain, with its covering, becomes more and more dilated anteriorly; it is followed by the three visceral arches corresponding to the three cranial vertebræ; and the heart, with the aortic arches, in consequence of the development of the cervical portion of the embryo, appears to retire beneath the shoulders.

In figures 202 and 203, *a*, indicates the "investing membrane;" *b*, the membrana intermedia; *b'*, the peripheral part of that membrane; *c*, the mucous membrane; *c'*, its peripheral portion; *f*, the branches of the aorta; *b''*, the space left by the separation of the laminæ of the amnion from the membrana intermedia; B, the lamina of the amnion; B', the visceral laminæ projecting downwards from the vertebral system.

Fig. 202.

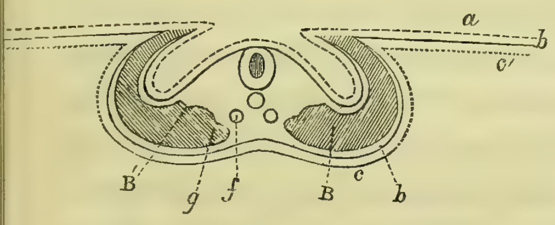
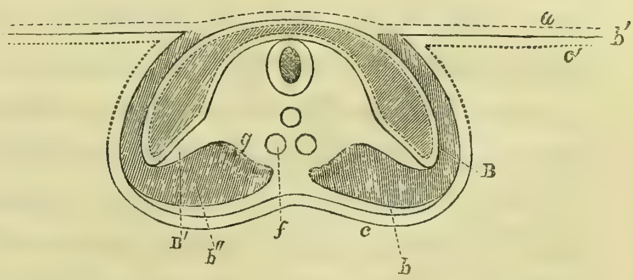


Fig. 203.



The visceral laminæ remain closely applied to the cutaneous system which, as membrana reuniens, is continued into the membrane of the amnion. The appearance of the visceral laminæ is the first step towards the closing of the abdominal cavity, in effecting which the cutaneous system precedes the visceral plates. The basis of the amnion extends inwards so as to embrace all the viscera of the abdomen, which are formed, or are in the process of formation, and in this way produces the umbilicus. Through the medium of this opening, which gradually grows smaller and smaller, the yolk, surrounded by the peripheral portion of the membrana intermedia, communicates with the embryo. In the abdominal region, therefore, the cutaneous system assumes its original function of membrana reuniens inferior, and it is followed by the visceral plates. The heart also becomes more completely enclosed within the cavity of the trunk by the extension backwards of the basis of the vagina capitis. The extremities also make their appearance at the anterior and posterior extremities of the abdominal cavity in the form of elevated ridges on the exterior of the visceral laminæ.

The Wolffian bodies and the allantois.—The Wolffian bodies, or larval kidneys of the embryo, show themselves at the sides of the aorta and its two divisions, extending in their known elongated form from the region of the heart to the caudal extremity of the embryo. Their situation, as seen in a transverse section, is indicated by the letter *g* in the two foregoing figures. Their development causes a still greater narrowing of the connection between the membrana intermedia and the vertebral system: the extent of the connection being now limited to the space between the two corpora Wolffiana. The lateral portions of the membrana intermedia are at the same time pushed downwards, and hang in the form of inclined planes from the middle of the body. (These are the laminæ of the intestinal canal, pointed out in fig. 203 by the letter *b*.) At the period when the rudiments of the corpora Wolffiana are pretty distinctly marked out, the amnion already nearly closed, indications of the extremities visible, but the insulation of the intestinal membrane not yet commenced; then, at the posterior extremity of the Wolffian bodies, and between the visceral plates, which are continuous with each other at this part, and the membrana intermedia, which is now depressed to some distance from them, there appear two prominences, at first separated by the bending downwards of the caudal extremity of the embryo. These prominences are at this time perfectly solid bodies applied closely to the corpora Wolffiana, and at the inner border of the latter organs a delicate streak or thread can be traced down to each of the bodies in question. These threads are the excretory ducts of the Wolffian bodies; and the two solid bodies connected with them are the rudiments of the allantois. The latter bodies gradually approach each other and coalesce, forming a prominent mass, of which the surface is at first flattened. This mass increases in size rapidly, and becomes developed to a closed sac. The further changes which this sac undergoes, and the vascular system belonging to it, are already well known. In consequence of the development of the allantois, the "investing membrane" of the ovum and embryo is removed to a distance from the amnion, and from the peripheral part of the membrana intermedia, which, by degrees, extends so as to embrace the whole yolk. According to these observations, therefore, the allantois is produced neither from the mucous membrane, nor from any part of the intestinal system, which at this period is not at all marked off and formed, but is developed by the growth of cells at the posterior extremity of the corpora Wolffiana.

Rudiment of the liver and pancreas.—The mass from which the liver and pancreas are to be formed first shows itself when the central portion of the membrana intermedia begins to be separated by a constriction from the peripheral portion. This constriction of the membrana intermedia commences anteriorly, where the membrane is connected with the cephalic portion of the visceral cavity, which had become separated from the general cavity of the yolk-sac at an early period. It gives rise to the formation of a cavity, which afterwards is converted into the stomach. This cavity opens posteriorly into the yolk-sac; it is formed by the central portion of the membrana intermedia. Above it runs the aorta, and beneath it lies the posterior extremity of the heart. Also, inferiorly, but yet at the surface of the membrana intermedia, close to the place where the vitelline veins enter the heart, there appear two elevations,—at first of equal size,—the lobes of the liver; and besides these, also, the formative mass for the pancreas. These rudimentary masses have no kind of communication with the cavity of the central portion of the membrana intermedia, but are merely cellular growths from the surface of that membrane, from which they may be removed without its cavity being implicated. While the mass of the rudimentary liver and pancreas increases, and gains a connection with the main trunk of the vitelline vines, the membrana intermedia has gradually separated itself from that mass, and now proceeds to the last act of its formative power,—namely, to the development of the intestinal system. The original connection of the membrana intermedia with the rudimentary liver and pancreas ceases at an early period, and the development of those organs proceeds independently. In the liver the production of new cells is very active, and is the cause of its growth. But even at a later period, when the growth of the organ is only proportionate to that of other parts, this production of new cells continues, and in all parts of the organ cells are met with, which contain nuclei and young cells in all stages of development, just as in the frog. May not these young cells serve to increase the mass of the blood-cells?

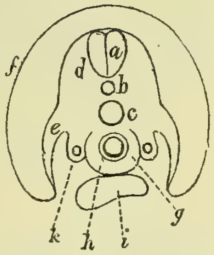
At the same time with the liver, the lungs also appear in a rudimentary form. They are at first flask-shaped masses of cells, lying one on each side of the cavity already described as being formed within the central portion of the membrana intermedia, and above the liver near the vertebral column. They may be traced forwards to that part where the cephalic division of the visceral cavity ceases, and they are there lost in the formative substance. From the situation of these rudimentary lungs close to the free surface of the membrana intermedia in the abdominal cavity, they almost appear as if they had been developed from that membrane; but the real source whence they are produced is the posterior part of the cephalic division of the visceral tube.

Intestinal system.—We make a distinction between the mucous membrane, the central organ of vegetative life, and the system of membranes connected therewith. By intestinal system we here would designate the latter structures. In the earliest period of the development of the embryo, the cephalic division of the intestinal system was withdrawn from the influence of the mucous membrane by the folding in of that part of the membrana intermedia, and its separation from the general yolk-cavity by a constriction. The cephalic portion of the visceral system thus became placed under the exclusive influence of the animal system. The cavity of the cephalic portion of the visceral tube becomes the mouth, pharynx, and œsophagus, and into it the respiratory apparatus opens as an appended structure.

In the shallow groove which the visceral laminæ at first bound in the abdominal region, lies the central part of the membrana intermedia, continued anteriorly into the cephalic portion. Between it and the visceral laminæ on each side run the Wolffian bodies. The lateral halves of the membrana intermedia increase in thickness, and show a tendency to coalesce. Their union commences anteriorly, then takes place at the posterior part, and lastly at the intervening part. Previously the central portion of the membrana intermedia formed, together with the peripheral portion, merely a part of the general periphery of the yolk-ball; but when the process of development which we are describing commences, the centre of the membrana intermedia raises itself above the mass of the yolk in the form of a roof of two inclined planes. These planes meeting at an angle beneath the vertebral column of the embryo, they are connected with it through the medium of the aorta and its two main branches. The lateral portions of the centre of the membrana intermedia gradually bend inwards at their lower margin, so as to convert the angular space or groove between them into a canal, which in the middle communicates by a wide opening with the yolk-cavity. By degrees the opening becomes narrowed, and at length is reduced to a very small passage, while the cavity of the canal (the intestine) grows larger.

The formation of the intestinal canal and the narrowing of the orifice of communication between it and the yolk-cavity, are succeeded closely by the closing of the visceral cavity in the abdominal region. This is effected by the extension inwards of the base of the amnion, as membrana reuniens inferior, followed by the visceral laminæ. In this way is formed the umbilicus, at first of large diameter, from which the amnion now appears to take its rise.

Fig. 204.



In figure 204, *a* represents the central parts of the nervous system; *b,* the chorda dorsalis; *c,* the aorta; *d,* the parietes of the body continued superiorly into the dorsal laminæ; *e,* the visceral laminæ; *f,* the amnion; *g,* the intestinal membrane; *h,* the cavity of the stomach lined with mucous membrane; *i,* the liver; and *k,* the Wolffian bodies.

Fig. 205.

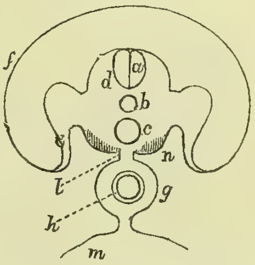
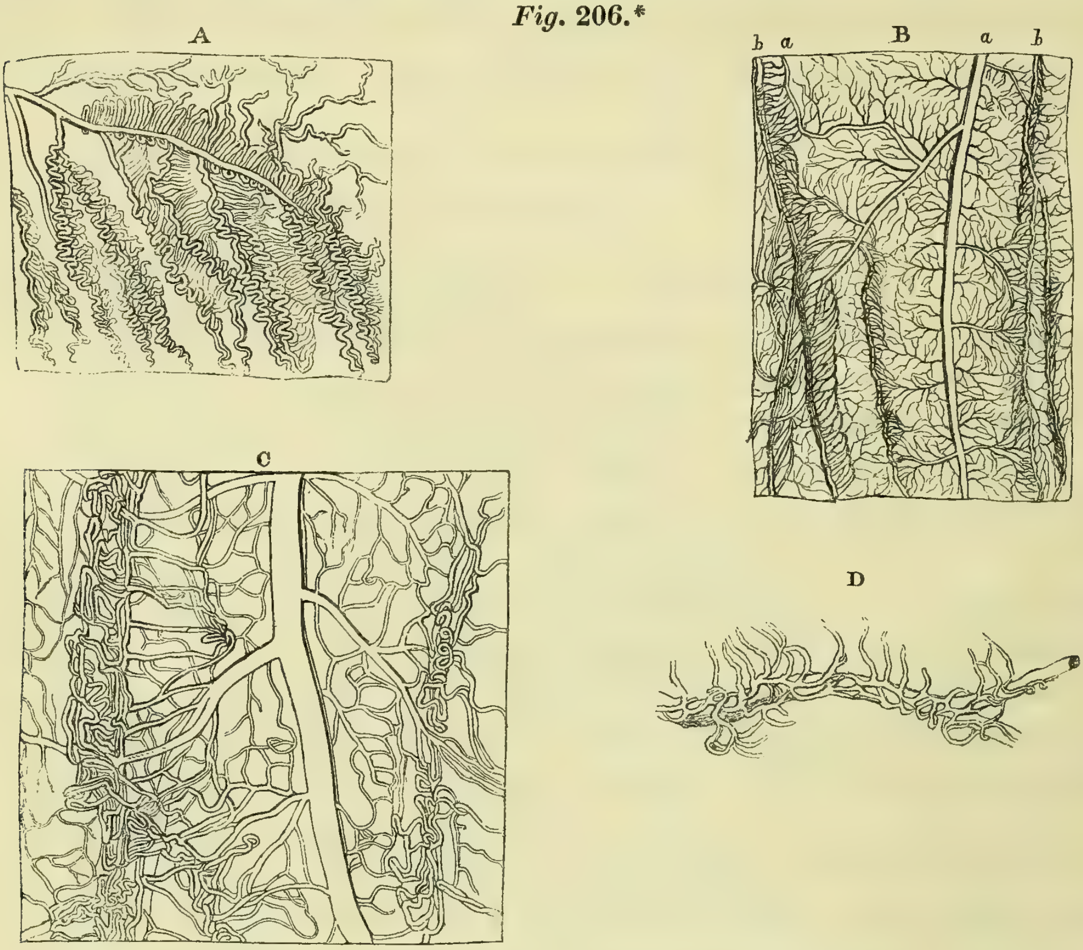


Figure 205 represents a section of the embryo in the neighbourhood of the upper extremities. *a* indicates the spinal cord; *b,* the chorda dorsalis; *c,* the aorta; *d,* the dorsal laminæ; *e,* the visceral laminæ; *f,* the amnion; *g,* the intestinal membrane; *h,* the cavity of the stomach with the mucous membrane; *l,* the mesentery; *m,* the yolk-sac; and *n,* the Wolffian bodies.

The mesentery is formed in exactly the same manner as in the frog. With the exception of the chorda dorsalis, of which the existence is only temporary, the mucous membrane is the only structure of the fœtus of equal importance, that is formed, extended, and even perfected independently of the vascular system. It receives its external investments from the central portion of the membrana intermedia. The peripheral portion of the latter membrane has gradually extended itself over the whole yolk, and invests it, except at a small round spot. The cortical layer of the yolk becomes closely connected with the peripheral portion of the membrana intermedia. The vitelline arteries extend from this cortical layer into the yolk, forming the vascular loops known as the "vasa lutea." The function of the yolk itself is now reduced to that of mere nutritive matter, and the contents of the yolk-cells have undergone an essential change, since they yield under pressure a coherent fatty substance. [For the most recent observations on the subjects treated of in this chapter, see the Appendix.]

[The translator is indebted to Mr. Grainger for the following observations on *the structure and functions of the umbilical vesicle of the chick.* "When examined in the early days of incubation, the inner surface of the umbilical vesicle, composed, as it appears, of a highly organised mucous membrane, presents a surface uniformly extended, with no folds or inequalities perceptible by the naked eye, except those caused by its blood-vessels, which are most abundant. Subsequently an immense number of folds or valves, as they were termed by Haller, become visible, and on the ninth day of incubation they are very much developed and project into the altered yolk. These folds become gradually more and more developed, and are doubled on themselves in a most intricate manner, especially after the chick has left the shell. (See fig. 206, A.)

Fig. 206.*



In proportion as the vesicle diminishes in size, from the absorption of its contents, the folds are more crowded together. On the nineteenth day their extreme depth averages five-twelfths of an inch, gradually tapering off to a line or less in depth. When the inner surface of the vesicle is viewed under the microscope with a low power, it is seen to be covered both on the valves and in their intervals with an immense number of greyish-white corpuscules. Mr. Dalrymple has discovered that these globules may, by careful washing, be entirely removed, and that when this is done, after a successful injection of the omphalo-mesenteric vessels, the branches of these vessels, which form the folds above described (see fig. 206, B.) appear, so far as colour is concerned, like other blood-vessels; the peculiar colour which induced Haller to apply to them the name of *vasa lutea* being entirely dependent on the layer of granules covering them. I have lately had an opportunity, through the kindness of my friend Mr. Dalrymple, of examining some most perfect injections of the umbilical vesicle. The following is our joint account of the microscopic characters of the *vasa lutea*:—There are two classes of these vessels. The more simple form anastomoses on the plane part of the umbilical vesicle, principally between the valves. The second set consists first of all of a trunk lying in the bottom (or free border) of the convoluted (wavy) fold or valve, closely covered on its walls by a reticulum of smaller vessels, and having appended to it simple vascular loops, which appear to arise from and return into the main canal. (See fig. 206, C and D.) These loops are in free connection with each other, having free inosculations. The intricacy of the vessels in the valves is much increased in consequence of each valve necessarily consisting of two layers, and being arranged in a waving or serpentine form. The general result of this organization — that is, the frequent looping and anastomosis of the venules, and the folding of the valves—is to increase immensely the surface or extent of the venous system. That the vessels in question are veins is rendered very probable by their size, and by the functions known to be performed by the veins of the vesicle; indeed I have distinctly traced a direct continuity between the so-called vasa lutea and the omphalo mesenteric vein. The microscopic measurements of the different vessels of the umbilical vesicle here described are, according to Mr. Dalrymple, as follows: — The main trunks of the naked vessels (the arteries), seen in figures B and C, and indicated by *a* in figure C, measured $\frac{1}{135}$ of an inch in diameter; the vessels of the capillary network of the plane or intervalvular surface of the membrane, $\frac{1}{1080}$ of an inch; the trunks of the vessels covered with capillaries (the veins), (see fig. 207. B, *b*, and D,) where they emerged from the folds, $\frac{1}{90}$ of an inch (one-fourth of this diameter being due to the covering of smaller capillaries); and the capillaries forming the network of the folds about $\frac{1}{900}$ of an inch. In these injected specimens, when the granular matter had been completely washed away, there certainly was nothing resembling a mucous membrane; the vessels, in some places especially, appeared quite free and uncovered towards the interior of the vesicle. It therefore is a question whether the granulated layer was the mucous membrane in an early stage of formation, a supposition which Mr. Dalrymple thought supported by the fact that some of the corpuscules were nucleated, and thus resembled the elementary condition of all tissues, or whether the mucous membrane had been destroyed in making the preparation.

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* [Figure 206. The folds of the vitellary membrane and the vasa lutea, after drawings by Mrs. Holmes from injections by Mr. Dalrymple. A represents the wavy folds before the layer of nucleated cells has been removed; B shows the vessels of the folds and of the membrane between them, laid bare, and more highly magnified; C is a view, with a still higher magnifying power, of the internal surface of a portion of the vitellary membrane, in which the arrangement of the vessels forming the folds is more accurately seen. D represents a portion of one of the venous trunks which lie in the free border of the fold, covered with its capillary network.]

" *Contents of the umbilical vesicle.*—As incubation proceeds, the yolk becomes liquefied, and, as Prout has shown, and I have myself ascertained, chemically changed by an intermixture with the albumen, which probably enters the yolk-sac by endosmose. The liquefaction of the yolk always takes place at that part where it is covered by the vasa lutea; so that whilst a portion drawn out by a syringe in this situation is fluid, and does not coagulate by the ordinary tests, the yolk below is unaltered, and readily coagulates.

" *Functions.*—The umbilical vesicle is the organ on which the embryo of all classes is dependent for the materials of its development in the first period of existence, whilst in the oviparous and ovoviviparous animals the whole of the nutritive matter is derived from this source. The opinions which have prevailed respecting the mode in which the nutriment is introduced into the body of the embryo are extremely vague, and apparently erroneous. Some writers have attributed the nourishment, in part at least, to absorption of the albumen by the allantois; but all, with various modifications, contend for the introduction of nutritious matter into the intestine by the vitelline duct; whilst the agency of the vasa lutea is admitted, more or less, at one or other epoch of incubation. I believe it to be susceptible of proof, however, that instead of there being three different modes of nourishing the embryo, there is in the oviparous and ovoviviparous animals but one, that one consisting of the beautiful apparatus of the omphalo-mesenteric blood-vessels, with their appended plexus of the so-called 'vasa lutea.'

" The principal facts which support this view are, 1. that the vasa lutea do not disappear or decrease in proportion as the vessels of the allantois grow larger, but, on the contrary, become more and more developed, and at the end of incubation cover the whole yolk. 2. That they persist until the whole of the contents of the vesicle have disappeared, and are present after the ductus vitello-intestinalis has become impervious; the following being the order of disappearance of these parts; first, the vitelline duct; second, the contents of the vesicle; and last of all, the omphalo-mesenteric vessels. 3. That the action of these vasa lutea, consequently, continues until the whole of the process of development, so far as the egg is concerned, has come to a conclusion. 4. That the new nutritive compound formed within the umbilical vesicle by the union of the yolk and albumen, always accumulates at that part of the vesicle which lodges the vasa lutea. 5. That the opinion of the transmission of the contents of the umbilical vesicle into the intestine by the vitelline duct has apparently been adopted from two circumstances, namely, the open condition of that duct, and the supposed presence of yolk in the intestine of the embryo. But that these circumstances are inconclusive; in the first place, because the duct is closed before all the contents of the vesicle are absorbed, while its open condition, a necessary result of the organic formation of the intestinal canal from the upper part of the umbilical vesicle, no more indicates a functional action, than does the tube of the urachus resulting from the formation of the allantois and urinary bladder; and in the next place, because the presence of a substance resembling yolk in the intestine has been very rarely observed, and, in many of the instances in which it has been seen, has probably consisted of a mixture of bile and mucus like the meconium. 6. That the office of the allantois is, to serve the function of respiration, and not to absorb nutriment."]

CHAPTER III.

DEVELOPMENT OF MAMMIFEROUS ANIMALS AND MAN.

1. *Development of the ovum of Mammalia.*

THE transit of the ovum from the ovary into the Fallopian tube sometimes takes place within a few hours after the act of sexual union: thus, Dr. Barry found that the ovulum of the rabbit left the ovary within nine or ten hours after the coitus. In other cases the process occupies twenty-four hours, or even several days.

De Graaf* observed that the ovula of rabbits had been discharged from the ovary three days after the coitus. Cruikshank† found them in the Fallopian tube on the third day, and on the fourth day in the uterus. Coste found ova of rabbits in the uterus twenty-four hours after sexual union. Wharton Jones detected the ova of a rabbit in the Fallopian tube two days after impregnation; while in a rabbit which he examined forty-one hours after its connexion with the male, no ova could yet be discovered either in the tubes or in the uterus. Prevost and Dumas, instituting an examination of two bitches eight days after impregnation, found ova in the uterus; and in one of the two a single ovum was also discovered in the Fallopian tube.

According to the researches of Bischoff, made on bitches, the period of the escape of the ova from the ovary is very different in different cases. The earliest time at which he detected ova external to the ovary was thirty-six hours. In one bitch the ova had not left the Graafian vesicles nineteen hours after the act of sexual union. In another bitch, which fourteen days previously had ceased to have coitus with the dog, the ova had reached only the middle of the Fallopian tubes. A third bitch had refused the dog eleven days, and yet the ova had only just entered the uterus, and were very backward in their development. A remarkable fact, which seems quite unique, has been observed in the case of the ovum of the roe-deer. A very long period intervenes between the act of impregnation and the separation of the ovum from the ovary. The time of sexual union is August, while, according to the numerous observations of Pockels,* the ovum does not leave the Graafian vesicle and enter the Fallopian tube before December. The period of heat lasts from the end of July to the end of August. The ovum therefore remains about four months after its impregnation before its development commences.

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* Opera Omnia, p. 215.

† Phil. Transact. 1797.

The primitive changes which the ovum undergoes in the Fallopian tubes, and in the uterus, have been described by Cruikshank, Prevost and Dumas, Von Baer, Coste, Wagner, Wharton Jones, Bischoff, and Barry.

As early as 1672, De Graaf † detected ova in the Fallopian tubes of the rabbit, and observed that they had two coats. He says, " Minutissima ova quæ, licet perexigua, geminâ tamen tunicâ amiciuntur." In ova of the rabbit, taken from the Fallopian tube on the third day after impregnation, Cruikshank believed that he could distinguish three coats. The rudimentary condition of the embryo, in which merely the primitive streak and the area pellucida are visible, was first observed by Prevost and Dumas ‡ in the bitch. The last-named physiologists have given no accurate description of the very early ova which they discovered in the cornua of the uterus of the bitch ; but in their drawings granules, containing each a nucleus-like point, are distinctly represented. These granules are stated to have existed at the upper surface of the ovum, but whether they were seated in its interior is uncertain, since Prevost and Dumas speak of the " decidua." They figure a round white spot as lying beneath the granules in question, and compare it to the " cicatricula." Von Baer examined ova taken from the uterus of the bitch before the formation of the embryo. They were composed of an external transparent coat, beset here and there with short villi or knots, the " membrana corticalis," and of an internal coat presenting circular markings, which, by a higher magnifying power, were seen to be circles of granules. (This appearance has been explained by Bischoff.) In each ovum a round opaque spot was also visible. Von Baer regarded the internal coat on which the granules were seen as the vitelline membrane: it is the same tunic which Coste believes to be the germinal membrane. The opaque spot was supposed by Von Baer to be the germinal membrane or germ.

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* Wiegmann's Archiv. 1835, 195. Müller's Archiv. 1836, 183.

† Op. Omn. 216.

‡ Ann. de Sc. Nat. III. Tab. v. Fig. 2, 3.

On the third day after impregnation, the ova found by Coste* in the uterus of the rabbit measured one line in diameter. Examined with the aid of the microscope, the external transparent membrane of the ovum, or the vitelline membrane, was perceived to be invested internally by a second granular membrane. The latter membrane enclosed the entire yolk, which at this period had become perfectly transparent. On the seventh day Coste detected the first rudiment of the embryo in the form of a spot composed of granular nebulæ, which lay at the surface of the granular membrane (the germinal membrane of Coste) and in its substance. The streak was distinguishable in this spot. In his more recent work,† Coste has related similar observations made on ova of the bitch, as well as of the rabbit, and has given drawings of the germinal membrane and the round embryo spot. He has also given similar representations of the germinal membrane of the sheep.

R. Wagner examined the ova of the rabbit at a very early period after impregnation, when they had reached the uterus but had not yet obtained any attachment. The ovum was of an oval shape, two lines in length, and one line and a half broad. It was composed of two coats; of which the more external one was quite transparent, structureless, and thinner than the "zona pellucida" of the unimpregnated ovum in the ovary. The more internal coat, which after the ovum had been placed in water was separated from the external coat by a distinct interval, had a layer of small globules on its inner surface. In the middle of the ovum Wagner could distinguish a spot, composed of granules which seemed to have coalesced into a membrane. This description agrees entirely with that of the ovum observed by Gurlt, and likewise figured by Wagner. With respect to the external tunic of the ovum, Wagner inclines to the opinion of Baer, that it becomes developed into the chorion, or the external membrane of the ovum in its more developed state. The second or internal tunic was regarded by Wagner as either the vitelline membrane or the germinal membrane, while he supposed the circular granular spot to be the germinal disk.‡

Wharton Jones found ova in the Fallopian tubes of a rabbit on the second day after impregnation. They were surrounded by a thick layer of gelatinous substance, which he found to exist even while the ovum was in the ovary, but which had not the form of a membranous investment until after impregnation. It is from this gelatinous layer, according to Wharton Jones, and not from the vitellary membrane, that the chorion is formed.*

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* Recherches sur la Génération des Mammifères, Paris, 1834.

† Embryogenie Comparée, Paris, 1837.

‡ Abhandl. D. K. Baiersch. Akad. II. 1837.

Valentin† and Dr. Martin Barry‡ also describe the ovum found in the Fallopian tube to be invested by a thin membrane (see fig. 207), which subsequently becomes the chorion. This membrane, according to their observations, is formed during the passage of the ovum through the Fallopian tube; and the villi of the chorion gradually become developed from it. The vitelline membrane, according to Barry, disappears by liquefaction.§

The interesting researches of Bischoff have afforded us a complete view of the successive changes which the structure of the ovum undergoes in its passage through the Fallopian tube, and during the period immediately following its reception into the uterus.

All the ova which Bischoff‖ found in the Fallopian tubes bore a remarkable resemblance to the ova taken from the ovary: they still had the granular germinal disk, and the earliest had undergone no change of size. The germinal vesicle was sought for in vain; although it was still present in ova taken from the tumid Graafian vesicles of the ovary of a bitch nineteen hours after the first coitus. In its passage through the Fallopian tube the ovum gradually increases in size and the yolk in consistence. The granules of the yolk escape from the ovarian ovum when it is injured; while the yolk of impregnated ova may, according to Bischoff, be divided into two, four, or six solid portions. Bischoff further observed that the mass of the yolk had separated at parts from the inner surface of the vitelline membrane, and had assumed an angular figure. In several ova which had nearly reached the end of the Fallopian tube, a very delicate membrane was perceived closely surrounding the yolk; but Bischoff denies that an external coat, destined to become the chorion, is added to the ovum in the Fallopian tube.* At the period when the ova of the bitch and rabbit reach the uterus, they are, according to Bischoff, from five to six times as large as they are in the ovary. The vitelline membrane, or external coat of the ovum, grows thinner in the same proportion as the yolk increases in size; and the yolk itself becomes at length more fluid and transparent. On the surface of the yolk a connected layer of granules or, more correctly speaking, of cells is formed. This is the germinal membrane: it invests the entire yolk, and presents on one side of it a roundish opaque spot. Bischoff found the ova at this period lying quite free in the uterus, not surrounded by any decidua; and the discus proligerus was no longer visible. The germinal membrane, according to the observations of Bischoff made on the ova of the bitch, consists entirely of delicate cells, including granules. The embryo spot also consists of cells. The cells of the germinal membrane soon become so closely pressed together, that they assume, for the most part, the hexagonal form. In the middle of the cells smaller bodies (nuclei) are now seen, and around these an irregular granular substance.

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* Phil. Transact. 1837.

† Repert. 3, 190.

‡ Philos. Transact. 1839, pt. ii. p. 339.

§ [It had been remarked by Valentin (Entwickelungs-geschichte, p. 39) that it would be interesting to know whether the mucous membrane of the Fallopian tube presents differences of structure at different parts for the secretion of albumen and chorion around the ovum, corresponding to the two divisions of the oviduct which secrete the albumen and membrane of the shell of the bird's egg. Mr. Grainger has observed that the Fallopian tube of Mammalia is really formed of two parts of very different structure. The following is an extract from an account of his observations communicated to the translator in writing:—"On slitting open the Fallopian tube of a sow a few days after conception, a decided difference was noticed in this canal. The part next to the uterus, 3¼ inches in length, had very thick coats like those of the vas deferens; the tube was very small, and was distinguished on its mucous surface by slightly elevated longitudinal rugæ. The second and more vascular part was 7½ inches long, and was suddenly enlarged, both as regards the outer surface and the canal within. It displayed a most beautiful and complex apparatus of folds or valves of the mucous membrane: these folds, like the striæ of the first portion of the tube, ran longitudinally, but owing to their great development had a plaited arrangement. I have since remarked the same difference, whenever I have sought it, in the tube of the cow, rabbit, and sheep." Lately Mr. Grainger has ascertained that it exists also in the human subject.]

‖ Wagner's Physiologie, p. 95.

Dr. Barry† has likewise observed these cells with nuclei and nucleoli. The first cells are, he says, large; but these are succeeded by smaller and more numerous ones. A continuous layer of cells forms at the inner surface of the membrane which surrounds the yolk; while a mulberry-like body is produced in the centre of the ovum. Dr. Barry has also instituted observations on the early stages of the development of the embryo, which seem to prove that the process in the Mammalia is in some measure peculiar.

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* [A further remarkable observation has more recently been made by Bischoff (Müller's Archiv. 1841, p. 14) on the mammiferous ovum in the Fallopian tube. In four ova, found in the Fallopian tube of a rabbit shortly after impregnation had taken place, he saw the yolk perform regular and energetic rotary movements within the cavity of the zona pellucida; and he also distinctly perceived that the surface of the yolk-mass was beset with delicate cilia. Bischoff has observed movements of the same kind, and also produced by cilia, in the ova of frogs, the yolk and embryo revolving within the vitellary membrane. The rotation of the embryo, by means of cilia in the ova of Mollusca and Polypi, has been long known; and the same phenomenon has been discovered by Ehrenberg and Von Siebold in the ova of Medusa Aurita. Bischoff's observations render it probable that the process is one common to all animals. Dr. Barry (Philos. Transact. 1839, pt. ii. p. 355) had previously described the rotatory motions of a mulberry like object within a vesicle which he found attached to the lining membrane of the Fallopian tube. He compared this object to the structure of similar form which he has discovered to occupy the centre of the mammiferous ovum in certain stages of its development, and remarked that it remained to be discovered whether the latter structure also performs rotatory motions as the embryos of Mollusca and Polypi are known to do. But he regarded the revolving body observed by himself, and the vesicle containing it, as identical with certain pellucid vesicles which he had frequently seen under the mucous membrane of the uterus of the rabbit.]

† Edinb. Philos. Journal, 1839.

[Dr. Barry's observations, of which Professor Müller had seen only a short abstract, appear to be not only highly interesting, but very important. In the account of his observations relative to the first changes succeeding fecundation (see page 1497), his description was followed up to the point where, the ovum having reached the middle of the Fallopian tube, the germinal vesicle disappeared and was succeeded by two cells. The further changes which Dr. Barry has found the essential parts of the ovum to undergo, up to the formation of the embryo, are as follow:—Each of the twin cells (fig. 207, A) gives origin to two others, making four (fig. 207, B): each of these four in turn gives origin to two, by which the number is increased to eight (fig. 207, C); and this mode of augmentation continues until the germ consists of a mulberry-like object, the cells of which are so numerous as not to admit of being counted (see fig. 207, D, E, F). Together, with a doubling of the number of the cells, there occurs a diminution of their size. Every cell, whatever its minuteness, is found filled with the foundations of new cells into which its nucleus has been resolved. These foundations of new cells are arranged in concentric layers around a pellucid point. Each cell in fact exhibits the same process of cellular development as the original parent cell — the germinal vesicle (see page 1497). The foregoing changes usually take place in the ovum during its passage through the Fallopian tube. When it has entered the uterus, a layer of cells, of the same kind as those forming the mulberry-like body, makes its appearance on the whole of the inner surface of the membrane which invests the yolk (see fig. 207, F). The mulberry-like structure then passes from the centre of the yolk to a certain part of that layer (fig. 207, G); the vesicles of the latter coalesce with those of the former, where the two sets are in contact, to form a membrane — the future amnion; and the interior of the mulberry-like structure is now seen to be occupied by a large vesicle containing a fluid and dark granules. In the centre of the fluid of this vesicle is a spherical body, composed of a substance having a finely granular appearance, and containing a cavity filled with a colourless and pellucid fluid (see fig. 207, H). This hollow spherical body seems to be the true germ. The vesicle containing it disappears, and in its place is seen an elliptical depression filled with a pellucid fluid. In the centre of this depression (which appears to correspond to the area pellucida of the bird's egg) is the germ still presenting the appearance of a hollow sphere (fig. 207, I).

From the germ the embryo now begins to be formed. The germ separates into a central and a peripheral portion, both of which, at first appearing granular, are subsequently found to consist of vesicles. The central portion occupies the situation of the future brain, and soon presents a pointed process (fig. 207, J and K). This process becomes a hollow tube, exhibiting an enlargement at its caudal extremity, which indicates the situation of the future sinus rhomboidalis. Up to a certain period new layers of vesicles or cells come into view in the interior of the central portion of the germ, parts previously seen being pushed further out (see fig. 207, L and M).

According to Dr. Barry, there is no structure in the mammiferous ovum entitled to be denominated the "germinal membrane." The "amnion" (indicated by the cypher 4 in fig. 207, K, L, M), is formed, as has already been mentioned, from an epithelium-like layer of cells which lines the investing membrane of the ovum, and from the outer cells of the mulberry-like body, which together constitute a layer corresponding to the "lamina serosa" of authors. The "vascular lamina" of the umbilical vesicle arises as a hollow process originating from the germ and extending beneath the amnion so as to include the yolk.]*

The observations and drawings of Prevost and Dumas have shown that the formation of the embryo of Mammalia takes place according to the same plan as that of birds. For they have figured the "primitive streak," the "dorsal laminæ" bounding it on each side, and the pear-shaped "area pellucida," just as they appear in the incubated hen's egg; only the area immediately surrounding the area pellucida, and, without doubt, destined to form the "area vasculosa," is peculiar, inasmuch as its very elongated form corresponds to that of the area pellucida. Von Baer † saw the germinal membrane in a vascular state, in an ovum taken from the uterus of a bitch. Wagner represents the vascular area in an ovum ‡ of the same animal of a circular form. The embryo bears the same relation to the entire sac-like germinal membrane in the mammiferous ovum as it does in the ovum of the bird. This was first shown by Von Baer, and the fact is illustrated by the beautiful drawings of Coste,§ taken from the rabbit, and of Bischoff,|| from the bitch. The "yolk-sac" of the mammiferous ovum communicates with the intestine of the embryo, at first by a wide opening, and afterwards by a duct or hollow pedicle, the "ductus omphalo-mesentericus," which is accompanied by the same vessels as in the bird, the "vasa omphalo-mesenterica." This yolk-sac of Mammalia is commonly called the "umbilical vesicle, or vesicula umbilicalis." According to Von Baer's researches, it has an external

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* Philos. Transact. 1840, pt. ii. p. 536, et seq.

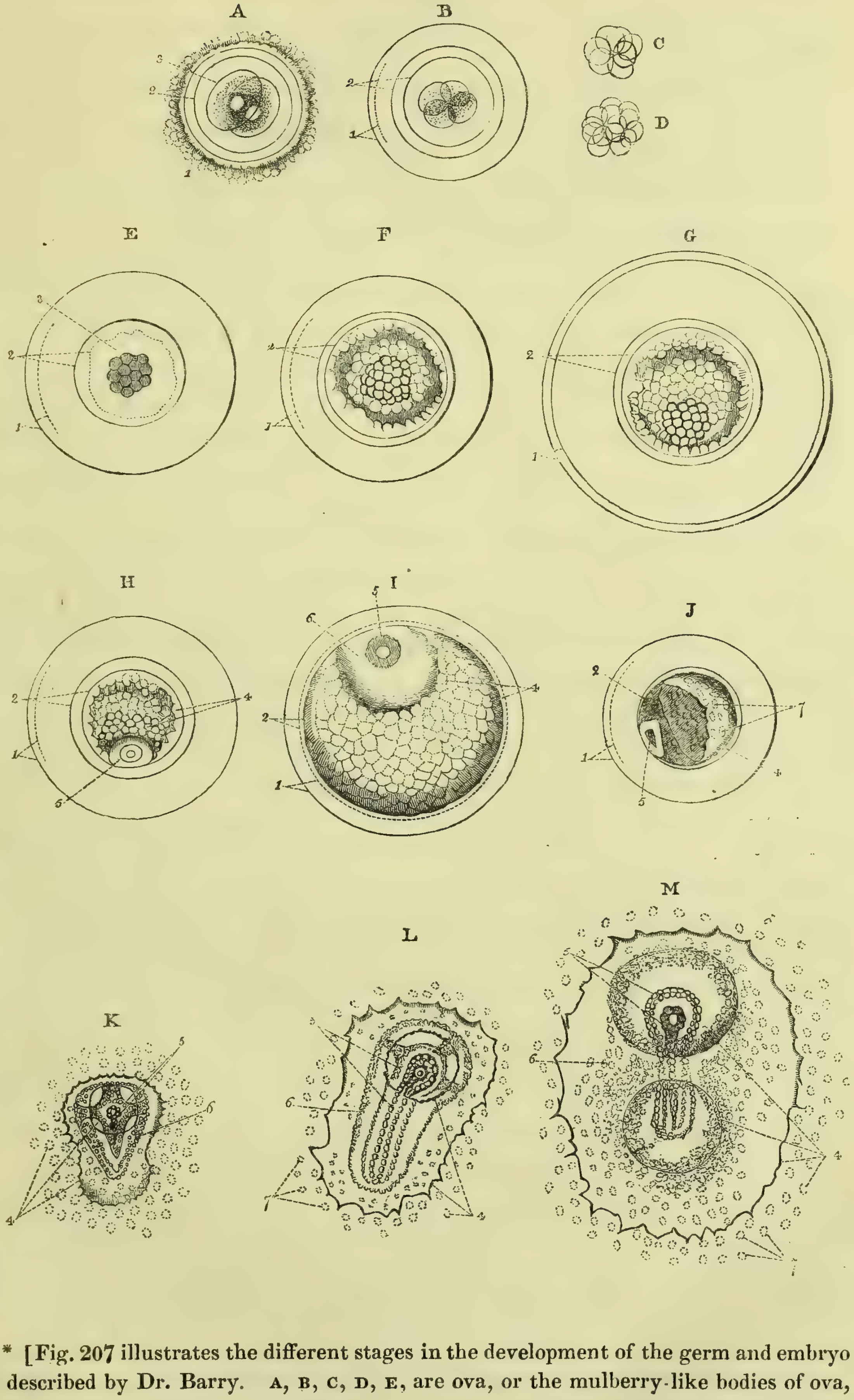
† De ovi Mammalium genere. Fig. vi.

‡ Icones Physiol. Tab. vi. Fig. 9.

§ Embryogenie. Tab. viii.

|| Wagner's Icones Physiol. vi. Fig. 11–14.

Fig. 207.*



* [Fig. 207 illustrates the different stages in the development of the germ and embryo as described by Dr. Barry. A, B, C, D, E, are ova, or the mulberry-like bodies of ova, found in the Fallopian tube, between its middle and the uterus, at periods varying from 24 to 63 hours post coitum. F, G, H, I, and J, are ova taken from the uterus

vascular layer, and an internal mucous layer, from which villous prolongations project into the yolk. These villi or folds, which are similar to those found in the yolk-sacs of birds, exist likewise in the umbilical vesicle of the human ovum. The "amnion" was observed by Von Baer to hold the same relation to the abdominal plates of the embryo, as in the bird; and it is doubtless developed in the same manner. The "allantois" also, is developed by the same process as in birds; its formation has been elucidated, more especially by the researches of Von Baer and Coste. Its blood-vessels are the "vasa umbilicalia."

Before the formation of the urinary bladder, the allantois communicates with the common reservoir, into which the excretory ducts of the Wolffian bodies, the ureters, and the organs of generation open, which is called the "sinus urogenitalis." The urinary bladder is developed from the apex of this cavity; and for a certain period it is continued into the pedicle of the allantois or the urachus. The amnion passing off from the margin of the umbilicus, and forming a bladder-like investment for the fœtus, encloses, as a sheath, all the parts which issue from the umbilicus; namely, the pedicle of the umbilical vesicle or yolk-sac, the vasa omphalo-meseraica, the pedicle of the allantois, and its blood-vessels, the vasa umbilicalia. (See fig. 208.) These parts are thus united into a common cord, the "funiculus umbilicalis;" and the sheath of this cord, the "vagina funiculi umbilicalis," is consequently formed by the amnion. Through the medium of the vessels of the allantois, the vascular system of the fœtus reaches the "chorion," in the substance of which, and in its villi, the allantoid or umbilical vessels ramify.

While the ovum is undergoing the first changes of development in the uterus, it lies quite free in the cavity of that organ. But subsequently an exudation is poured out upon the inner surface of the uterus which is composed of cells, and constitutes the thin "membrana decidua" of the mammiferous ovum. Into this membranous uterine production, which is especially distinct in carnivorous animals,* the villi, growing from the chorion of the ovum, become inserted. At a still later period, the ovum enters into another kind of union with the uterus, by means of the placenta, the structure of which will be described hereafter. [More recent information respecting the development of the mammiferous ovum will be found in the Appendix.]

at periods between 86 and 105 hours post coitum. K, L, and M, are embryos from ova of 111½ to 124½ hours. In all these figures, 1 indicates the incipient chorion; 2, the thick transparent membrane of the ovum or the zona pellucida; 3, the two cells into which the germinal vesicle and its contents become resolved, and the mulberry-like body which takes the place of those two cells; 4, the amnion; 5, the true germ; 6, (in fig. I,) the space corresponding to the area pellucida; 6, (in figs. K, L, M,) the peripheral portion of the germ; 7, the cells of the layer which becomes the vascular lamina of the umbilical vesicle.]

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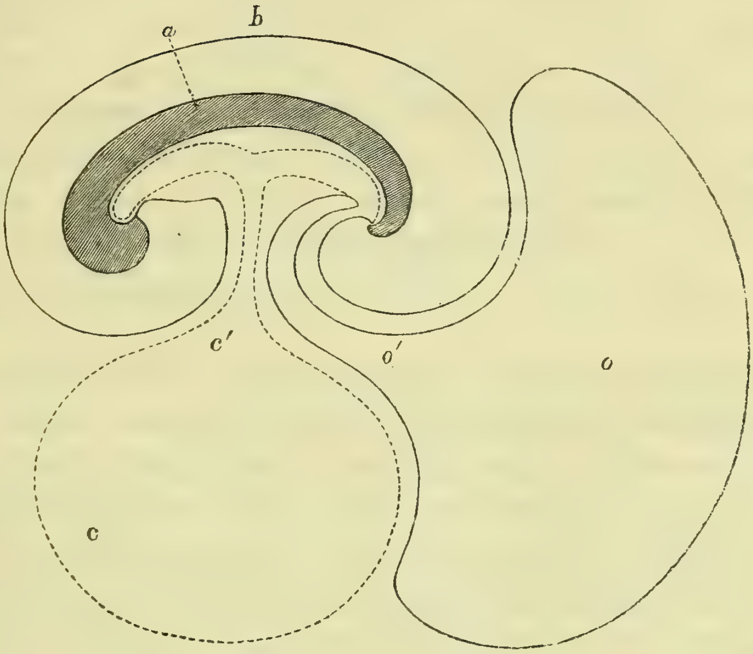
* Bojanus, loc. cit.

Fig. 208.*



The preceding description of the mammiferous ovum applies to the whole class of Mammalia, for in the ovum of all these animals there is an umbilical vesicle, an amnion, and an allantois. There is, however, a great variety in the relative development of the different parts in the different orders of the Mammalia. We will now briefly pass in review the most remarkable varieties of this kind; noticing, at the same time, the principal steps by which this branch of knowledge has been advanced.

Rufus Ephesius distinguished the amnion and its fluid from the allantois in the ovum of animals. Galen described, as existing in the ovum (of ruminants), an external tunic, which he called the chorion; a second belonging to the fœtus itself, called by him the amnion; and a third lying between the two former, and connected with the urinary bladder, through the medium of the urachus, which he denominated the allantois. G. Needham discovered the umbilical vesicle, which he named the fourth membrane, together with its accompanying vessels, arising from the mesentery, in the ova of the dog, cat, and rabbit. The uniform presence of these membranes of the ovum in all the Mammalia, and their agreement with those of the bird's egg, was first correctly and completely recognised by Oken and Kieser. They also correctly asserted the direct connection of the umbilical vesicle or yolk-sac of the mammiferous ovum with the intestinal canal, a structure which had been denied by many, the apparent connection having been supposed to be formed merely by vessels. Meckel afterwards refuted the opinion of Oken, that the cœcum was the point of connection of the umbilical vesicle with the intestine ; but still the fact of that connection really existing may easily be verified in very young embryos. Bojanus* demonstrated the connection of the vesicle with the small intestine in the dog. The same structure is uncommonly distinct in the ovum of ruminants in the earliest period of development (before the third week); and has been seen by Coste, as well as by Pockels, and myself. The hollow pedicle is, indeed, at this period, as wide as the elongated forked vesicle itself.

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* In figure 208, *a* represents the dorsal structures of the embryo; *b*, the amnion; *c*, the yolk-sac or umbilical vesicle; *c′*, the vitelline duct or pedicle of the umbilical vesicle; *o*, the allantois; and *o′*, the urachus.

The varieties presented by the development of the different parts of the ovum in the various families of the class Mammalia, and their nature, have been elucidated by Oken, Kieser, Dutrochet, Von Baer, and Coste. Von Baer has treated most fully of this part of embryology; and we shall, therefore, here chiefly follow the account which he has given. The ovum of some Mammals rapidly assumes an elongated form at the commencement of its development. This takes place to the least extent in the Carnivora, as in the dog; to the greatest extent, in the Solidungula, in which the ovum is drawn out at each extremity into a long horn. The yolk-sac or umbilical vesicle of the Solidungula, as well as of the Ruminantia, and hog, consists of a pedicle connected with the rudimentary intestine, which is, at first, of considerable width, and of two exceeding long cornua passing off from this pedicle or neck in opposite directions. The cornua, at a subsequent period, become atrophied, and only the middle portion is left in an active state, and supplied with vessels; but of this portion, at length, only a trace remains. The yolk-sac of carnivorous animals changes from a spherical to an ellipsoid, and afterwards to a fusiform or spindle-like shape, which it preserves until birth, acquiring a large size and retaining its vascular network. The yolk-sac of rodent animals does not become elongated into cornua ; but increases greatly in size, so that instead of being confined to the abdominal aspect of the embryo it extends between the amnion and chorion, over the dorsum of the embryo to the opposite side of the abdomen; it is persistent until birth.†

The allantois is, according to Von Baer, composed of two layers, of which the internal one is a prolongation of the mucous membrane of the embryo, and the other, the external vascular layer in which the vasa umbilicalia ramify. In carnivorous animals this sac bears a close resemblance to the same part in birds ; it extends entirely around the embryo, and invests the whole inner surface of the chorion, except at the part where the umbilical vesicle lies. That portion of the sac which lies in contact with the amnion, and which contains but few vessels, is the membrana media of earlier writers, and the "endochorion" of Dutrochet. The external portion of the sac, which is in relation with the chorion, is very vascular. The allantois of ruminants is from the first bicorned, and its cornua are developed in the same direction as those of the vesicula umbilicalis; but they retain their full size, while the cornua of the umbilical vesicle become atrophied. In the Solidungula the vascular layer of the allantois is separated from the mucous layer by an albuminous deposit; but in them, as well as in the Carnivora, where this separation does not take place, the vessels of the allantois ramify in the chorion. In rodents the allantois has its smallest size, and is confined to the abdominal aspect of the embryo; but its vessels soon leave it to ramify in the chorion. Here, therefore, as in other cases, the proper office of the allantois seems to be the conducting of the vessels of the embryo to the exterior envelope of the ovum, in which they ramify. Von Baer has demonstrated in the ovum of Mammalia a membranous layer lying beneath the chorion, which appears to correspond in origin to the serous layer in the egg of the bird. For it probably separates from the surface of the germinal membrane; then, as in the hen's eggs, grows in the form of a fold over the embryo, so as to form the amnion, and, after the completion and closure of the sac of the latter membrane, becomes isolated as a distinct lamella, enclosing the amnion, embryo, yolk-sac and allantois, and lying itself in close contact with the chorion. Between this lamella and the chorion there is, at first, a thin layer of albumen, the external albumen, which, however, passes by imbibition through the serous layer so as to collect beneath it, and then this layer appears to form merely a second lamella of the chorion. In ruminants, and in the hog, the allantois is free (as it in all cases is at first), and being rapidly developed soon reaches the serous lamella of the ovum and the chorion. It then extends into the long cornua of the ovum, and there at length bursts through the chorion, and protrudes, in the form of two cornua, externally. The extremities of the less elongated ovum of the Carnivora undergo the same change, and allow the cornua of the yolk-sac and allantois, still invested and held together by the serous covering of the ovum, to protrude. So soon as the vessels of the allantois have reached the chorion, they send minute branches into the villi of that membrane. Thus are formed the roots which henceforth extend from the surface of the ovum into the parieties of the uterus, and from which the placenta is afterwards developed.

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* Nov. Act. Nat. Cur. x. pt. i. p. 141.

† See Von Baer, loc. citat. p. 191.

Both the chorion and the amnion, according to the researches of Breschet and Gluge [and Barry], are composed of nucleated cells.

The fluid of the allantois contains the secretion of the primordial kidneys or Wolffian bodies, and of the true kidneys. Allantoin exists in it; and in that of birds Jacobson has discovered uric acid.*

2. *Development of the human ovum.*

The human ovum, in all probability, does not reach the uterus before the lapse of a week after impregnation. On the eighth day, Von Baer could detect no ovum either in the uterus or in the Fallopian tube. Home and Bauer state, that they found an ovum on the seventh day; but some doubt attaches to their observation. The ovum observed by E. H. and E. Weber was of the date of a week after impregnation. The earliest ova examined by Velpeau, belonged to a period between the tenth and twelfth days; they were already beset with villi, but presented no embryo. In an ovum of fourteen days Von Baer saw the embryo.

Before the ovum reaches the uterus, the formation of a new structure, the "membrana decidua," upon the inner surface of that organ, and corresponding, therefore, to its inner surface in form, has commenced. Ed. Weber observed it on the seventh day after coitus had taken place. It then resembled a layer of lymph, effused from the inner surface of the uterus, upon and between the enlarged vascular villi of that surface.† This membrane exists in animals also; but in a less highly developed form. It is sometimes formed in the uterus of the human female, in cases of extra-uterine fœtation, though not always; and in a case of development of the ovum in the Fallopian tube, the membrana decidua has been observed both in the uterus and in the tube. The membrana decidua is composed of a whitish grey, moist, and soft mass, similar to coagulated fibrin, and entirely formed of nucleated cells.‡ The vessels of the uterus are prolonged into this product. The thickness of the membrane sometimes equals from one to three lines. Its outer surface is intimately connected with the uterus, and when artificially detached, or separated spontaneously, is rough; while its inner surface is smooth. The relation which the decidua bears to the openings of the uterus is not always the same; it is sometimes closed at the lower orifices of the Fallopian tubes, and at the upper entrance of the cervix uteri; sometimes it is open at all these points or at one or other of them. R. Wagner* is quite correct in stating that all these varieties may occur. The cervix uteri is occupied by a mere gelatinous mucus.

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* The best figures of the ova of mammiferous animals will be found in the works of Von Baer and Coste, and in Gurlt's Anatom. Abbild. der Haus-säugethiere. The authors to be consulted on the subject of the development of this class are, Oken and Kieser, Beiträge Zur vergleichende Anatomie and Physiologie, 1806. Dutrochet, in the Mém. du Mus d'Hist. Nat. T. iii. p. 82. G. Cuvier, ibid. p. 98. Bojanus, Nov. Act. Nat. Cur. x. p. 1. C. Mayer, ibid. xvii. 2. Coste, Recherches sur la Génération des Mammifères, Paris, 1834, et Embryogenie, Paris, 1837. Von Baer, Entwickelungsgeschichte der Thiere 2te Theil. Burdach, Physiologie, Bd. ii. Valentin, Entwickelungs-geschichte. R. Wagner, Physiologie and Icones Physiologicæ.

† Disq. Anat. uteri et ovariorum puellæ, vii. a conceptione die defunctæ.

‡ See a notice, by the Author, on the cellular structure of the decidua in Schwann's paper, in Froriep's Notiz. 1838. No. 112. p. 22. See also R. Wagner, Physiologie, p. 114. and Icon Physiol. Tab. xi. fig. 5 and 6.

When the ovum enters the uterus, it becomes imbedded in the structure of the decidua which is yet quite soft. The earliest ova which have been observed in connection with the decidua, were not contained free in its cavity, but appeared to be implanted in it or pressed into it from without; the decidua, at the point of entrance of the ovum, being protruded inwards, and the ovum contained in a hollow of its external surface.† During the further growth of the ovum, the decidua becomes more and more inverted at this point, the inverted part being received into the cavity of the rest of the membrane. This inverted portion is called the decidua reflexa, while the other part of the membrane is called the decidua vera. The decidua vera and the decidua reflexa have the same structure, which differs totally from that of the mucous membrane of the uterus. They are, in fact, new products. It must not be imagined that the process by which the decidua reflexa is formed, is a mechanical one, that the ovum, as it enters the uterus, pushes the membrane before it; for, like all processes of the same kind, which occur in the animal organism, this one is effected by the vital vegetative action exerted in a determinate direction. The cavity of the decidua between the decidua vera and the decidua reflexa, contains an albuminous fluid, the "hydroperione" of Breschet. At the part where the uterine expansion of the decidua is interrupted by the reflexion inwards of the decidua reflexa, and where the ovum entered, the place of the former membrane is supplied by another mass similar to it, and connected at its margins with it, the "decidua serotina." When young ova are examined in the uterus, both the decidua vera and the decidua reflexa are generally found; but in aborted ova this is seldom the case, a part of the decidua being most frequently retained in the uterus. As the ovum increases in size, the decidua vera and the decidua reflexa gradually come into contact, and in the third month of pregnancy the cavity between them has quite disappeared. Henceforth it is very difficult, or even quite impossible to distinguish the two layers. During the further growth of the ovum the decidua becomes still thinner, but is not entirely lost. At birth a part of it remains behind in the uterus, while a part comes away, forming a thin membranous covering of the ovum.‡

The first connection which subsists between the ovum and the decidua, consists in the ramified villi of the chorion becoming imbedded in the hollow canals which traverse the decidua. The villi extend through these canals in the manner of roots, and thus draw nourishment from a maternal structure without having any organic connection therewith.

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* Meckel's Archiv. 1830, and Physiologie, p. 114–117.

† See Bock, de Membranâ deciduâ. Bonnæ, 1831.

‡ Respecting the decidua of the mature ovum, consult Bischoff, Beiträge zur Lehre von den Eihüllen des menschlichen Fötus. Bonn, 1834.

According to the recent researches of E. H. Weber communicated to me in manuscript, the decidua is composed in greater part of the tubular follicles, which lie very closely arranged at the inner surface of the uterus, and of numerous blood-vessels ramifying upon, and between them. In animals, the long tubular follicles, here and there bifurcated, lie in the substance of the uterus itself, and open upon its inner surface by numerous orifices.* In the human subject they form the decidua.† When the inner surface of the decidua is examined, numerous filaments can be seen in its substance, tolerably regularly disposed, and directed towards the surface. These filaments resemble closely set villi, except that they do not lie free; the interspaces between them being filled with the substance of the decidua. If the cut surface of a divided uterus is examined in the bright sunlight, with a lens, these supposed villi are seen to be long and thin cylindrical tubuli, which become somewhat narrowed where they reach the free surface of the decidua, while at the attached or uterine surface of that membrane they become wider, are much convoluted, and appear to commence by closed extremities. If the substance of a pregnant uterus is compressed, a thick whitish fluid exudes upon the surface of the decidua, similar to the secretion which may be expressed from the uterine glands of animals. The decidua presents at its inner surface numerous orifices, which have been long known, and which appear to be the mouths by which two or more of the tubuli open. Besides these, however, there must be many orifices of single tubuli which are not visible. The tubuli are almost a quarter of an inch in length, and here and there bifurcate; the branches being as wide as the trunk of the follicle. This character completely distinguishes them from the blood-vessels which run in contact with them; for the blood-vessels form a net-work or loops, or at all events ramify, diminishing in diameter at each division. The diameter of the follicles is about $\frac{1}{17}$ of a Paris line; that of the capillaries $\frac{1}{104}$ of a Paris line.‡

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* See E. H. Weber, in his Edition of Hildebrant's Anatom. Bd. iv. p. 505. Burckhardt, Obs. Anat. de uteri vaccini fabricâ. Basil. 1834. E. H. Weber, Annot. Anat. 186.

† Engraved representations of the Decidua will be found in Dr. Hunter's Gravid Uterus, Plates 33 and 34; in Velpeau's Embryologie, Paris, 1833; in Seiller's Gebärmutter und das Ei des Menschen in den ersten Schwangerschaftsmonaten. Dresden, 1832; in Kilian's Gehurtshülfl. Atlas. Tab. xxiv; and in C. Meyer's Icones Selectæ. Bonn, 1831. Tab. v. Figs. 6, 7, and 8.

‡ [Dr. Sharpey has been for some time engaged in investigating the structure and functions of the membrana decidua and the uterine glands, and has kindly favoured the translator with the following account of his observations:—

"The uterine glands alluded to in the text have now been ascertained to exist in

The development of the embryo, and the formation of the amnion and yolk-sac, are probably effected by the same process in man as in birds. The umbilical vesicle and its duct are known to have the same relation to the intestine as the yolk-sac and its duct have in the chick.

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several orders of mammiferous animals, and from their enlarged size and augumented secretion during pregnancy, as well as the peculiar connection which is then established between them and the fœtal membranes, it has been inferred that they are in some important way subservient to the nutrition of the fœtus. The uterine cotyledons of Ruminants were very generally considered to be of a glandular nature by the older anatomists and as destined to supply a nutrient matter to the fœtus; indeed, it had not escaped notice, that these bodies actually yield a mucilaginous secretion; but besides the cotyledons, Malphigi discovered glands opening on all parts of the inner surface of the uterus of those animals, and recognised them as secreting organs; he has described them, specially, in the gravid uterus of the sheep. (Opp. 1687, vol. ii. p. 220.) At a recent period the uterine glands of Ruminants were again observed by Baer, who also discovered similar glands in the sow, and although he erroneously supposed they were absorbent vessels, he described them well, and showed that they were connected in a peculiar manner with the ovum; the dilated orifices of the glands being attached to small vascular spots on the surface of the chorion, which, in the sow, he describes as formed by little circular or star-like elevations of the membrane surrounding a central depression. (Ueber die Gefaessverbindung zwischen Mutter und Frucht, 1828.) This arrangement was justly considered by Dr. E. H. Weber, who afterwards investigated the subject, as a provision for the accumulation of the secreted matter of the glands and for securing its effectual exposure to the blood-vessels of the fœtus. Weber also more fully described the glands in Ruminants, and observed glands of the same nature, though of a different form, in the uterus of the rabbit (loc. cit.). Still more lately uterine glands have been discovered in the pregnant Porpoise, by Dr. Eschricht of Copenhagen; and in the gravid uterus of the cat the same observer found oblong cells lying under the mucous membrane, which he considers to be glandular cavities, though he could not discover their orifices on the inner surface of the membrane. (De organis quæ resp. et nutr. fœtus mammal. insurviunt. Hafn. 1837, p. 43.) Having had occasion to observe these glands in the uterus of the bitch, and having examined their condition in various stages of pregnancy as well as their relation to the membranes of the fœtus, I beg to subjoin an outline of my observations.

Fig. 209.*

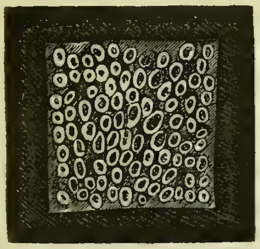
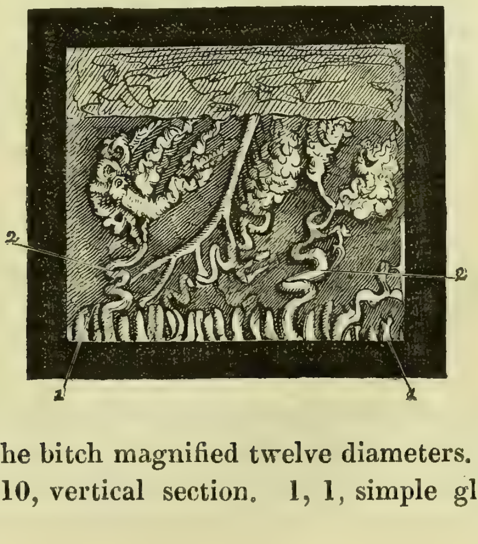


Fig. 210.*



* Figs. 209 and 210. Uterine glands of the bitch magnified twelve diameters. Fig. 209, openings on the inner surface. Fig. 210, vertical section. 1, 1, simple glands; 2, 2, compound ditto.

Hence the vesicula umbilicalis and the yolk-sac are to be regarded as completely identical. The connection of the umbilical vesicle with the intestine in the human embryo cannot be demonstrated with great distinctness at the period when the duct of the vesicle has already become

The glands of the mucous membrane of the bitch's uterus are of two kinds, simple and compound. The simple glands, which are the more numerous, are merely very short unbranched tubes closed at one end (fig. 210, 1, 1); the compound glands, (2, 2,) have a long duct dividing into convoluted branches ; both open on the inner surface of the membrane by small round orifices (fig. 209) lined with epithelium and set closely together. After impregnation the parts of the mucous membrane which come into immediate relation with the ova, together with the glands seated in those parts, undergo a remarkable alteration. In a uterus between three and four weeks after conception, at which period the dilatations or chambers (fig. 211) which contain the ova have attained the size of a walnut, we find, on laying open one of the chambers, that the lemon-shaped ovum is surrounded by a broad belt or zone of villi which rise from the surface of the chorion, and becoming vascular, take part in the formation of the zonular placenta. Corresponding with this there is a zonular portion of the inner surface of the uterus (fig. 211, 3), somewhat raised above the rest, and perforated with small pits, into which the fœtal villi are received, and as this part of the membrane enters into the formation of the placenta and comes away with the ovum at parturition it is justly regarded as the decidua. The decidua is no new structure, however ; it is merely a portion of the mucous membrane become more thick and vascular than the rest, and the pits on its surface which receive the fœtal villi are merely the glands already mentioned (fig. 209), somewhat enlarged and widened. While, however, the simple glands merely undergo a uniform enlargement, a change takes place in the compound glands of a much more remarkable character. The long excretory ducts of those glands (fig. 210, 2), immediately before they open on the inner surface of the membrane, become dilated into cells, one for each gland (fig. 213 and

Fig. 211.*

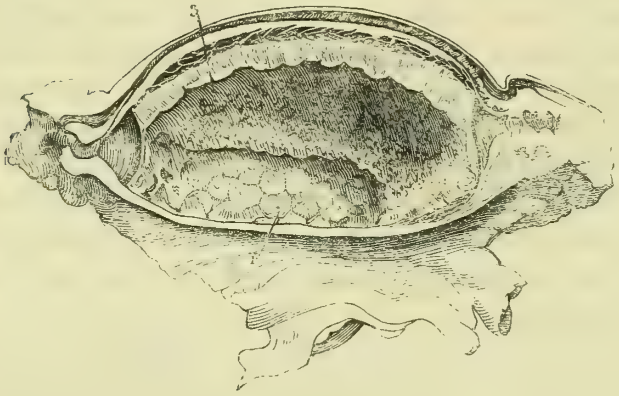
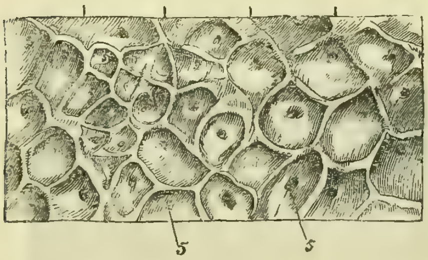


Fig. 212.†



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[*] Fig. 211. Natural size. A fœtal chamber of the uterus opened, the ovum removed. 3. Decidua with its perforations. At 4, part of the decidua has been removed to show the cellular dilatations of the glands beneath it.

[†] Fig. 212. Some of the glandular cells exposed as at 4 in former figure, magnified three diameters. 5, 5, the ducts opening into the bottom of the cells.

long and thin. Kieser* traced this duct to the intestine, and has given a representation of the structure. It was, however, the subject of much controversy, and the duct was by some anatomists regarded as a mere blood-vessel. In very young embryos, however, the fact may be demonstrated with certainty. In ova, in which the embryo measures

214, 4′), which are filled with a semi-fluid whitish granular secretion, and are lined with epithelium. These cells form a layer beneath the surface of the decidua (fig. 211, 4 ; fig. 213, 4′), and being crowded together assume a polyhedral form (fig. 212); at the bottom of each the tubular duct (figs. 212 and 214, 5) may be seen about to expand into the cell, and the cell again contracts at its orifice.

Fig. 213.†

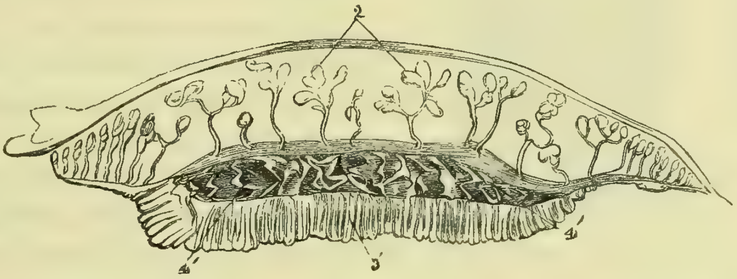
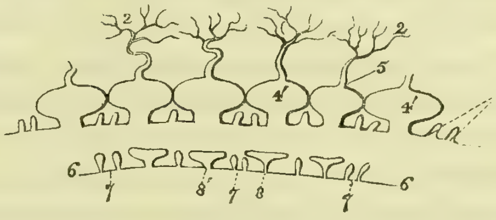


Fig. 214.‡



In a somewhat more advanced stage the glandular cells enlarge, their orifices expand, and now membranous processes (figs. 214 and 215, 8, 8′,) rise from the surface of the ovum and enter the glandular cells, passing a little way beyond the orifices, by the circumference of which they are embraced. These fœtal processes are prolonged from the chorion (6) and its vascular lining or endochorion (6′) and hence contain ramifications of the umbilical vessels. They are for the most part hollow or saccular, at least at first, and some of them present, for a time, a small aperture of communication (8′) between their cavity and the general sac of the chorion, or rather of its vascular lining, but this is soon obliterated ; ultimately, they come to resemble much the villi in structure, differing only in size and form. As pregnancy advances the parts described enlarge, the villi become more complex by ramification, the fœtal processes also give off numerous lateral offsets ; but their broad flattened tops which close the mouths of the glandular cells are smooth and even, and are covered with a prolongonly from two to three lines in length, the duct of the umbilical vesicle is very short and wide, and its walls are distinctly continuous with those of the rudimentary intestine. I observed this relation of the parts in an ovum which I described some time since.* Similar observations

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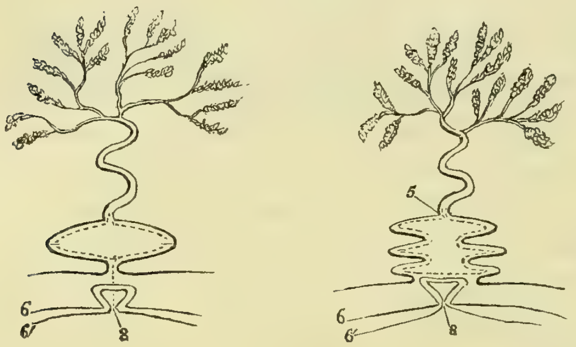
* Die Bildung des Darmcanals aus der Vesicula Umbilicalis. Götting. 1810.

† Fig. 213. Nat. size. Vertical section of parietes of a fœtal chamber somewhat more advanced than 211. At 2, the membranes have been drawn asunder to show the compound glands spread out. 3′, decidua. 4′, 4′, glandular cells.

‡ Fig. 214. Diagram of part of the decidua and ovum separated, to show their mutual relation. 2, 3, 4, 5, as in the former figures. 6, chorion. 7, villi. 8, 8′, fœtal processes of the chorion.

Fig. 215.



ation of the same epithelium which lines the cells (fig. 215 dotted line). The maternal or decidual vessels are everywhere closely applied to the surface of the villi and fill up the intervals between them : they also closely embrace the fœtal processes, except at their expanded summits, which, as before stated, are in contact with the secretion of the glandular cells. The maternal vessels in proceeding from the uterus first ramify on the parietes of the cells, by which they are supported ; but as they approach the villi and surface of the ovum they form an abundant network, the branches of which are unsupported by membranous structure, seemingly as if the intermediate tissue of the decidua had dissappeared, its vessels alone remaining in the later periods of pregnancy. At parturition the decidual vessels come away with the ovum, the parietes of the now greatly enlarged glandular cells also separate in great part from the uterus, leaving merely the bottoms with the round openings of the glandular ducts in their centres. After separation of the ovum and placenta, numerous truncated and somewhat shrivelled vessels project from the inner surface of the uterus ; they are chiefly veins, and they may be seen for a considerable time after parturition on those parts of the uterus to which the ova had been attached.

From the description given, then, it follows, that in the placenta of the bitch there is an arrangement by which a matter secreted from the enlarged glands of the uterus is brought into proximity with the vessels of the fœtus, and seeing that a provision of a similar nature is found in various other instances, it is not improbable that in viviparous animals generally a matter deposited from the maternal system by means of a glandular apparatus may be absorbed into that of the fœtus and serve for its nutrition ; but this is a question which can be determined only after a more extended investigation. As connected with this subject the source of the well known green-coloured deposit found at the borders of the placenta of carnivora would naturally become an object of inquiry, but on this point I cannot as yet speak with certainty.

Human Decidua.—These observations on the decidua of the dog led me to examine anew the human decidua, and more especially its relations to the mucous membrane of the uterus, and I shall now briefly state the result, although I find I have been in a great measure anticipated by Weber, as appears from the statement of Professor Müller in the text. It is right to mention, however, that the results were arrived at quite independently of Weber's observations, and, indeed, before the original of the pages of this work in which they are noticed reached me.

In various instances in which there was reason to believe that impregnation had recently taken place, and in which the ovary contained a recent corpus luteum and the uterus a distinct decidual lining, though no ovum had been discovered, the decidua, in some places $\frac{1}{10}$th of an inch thick, seemed obviously to consist of the thickened mucous membrane. Its surface presented a multitude of small round apertures (fig. 216), have been made by Wagner and Dr. Allen Thomson. The latter anatomist has indeed seen the umbilical vesicle at so early a stage of development, that its walls were, without any constriction, directly continuous

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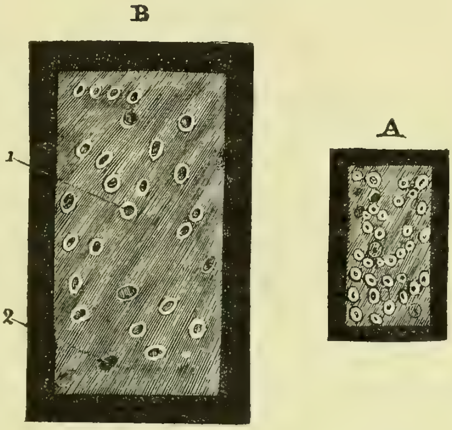
* Müller's Archiv. 1834, p. 8.

Fig. 216.*



which, on a vertical section, were seen to belong to the tubular glands of the mucous membrane, elongated, and enlarged. These tubes were lined with a white epithelium, (as at 1,) which rendered them very conspicuous; they were much waved and contorted towards their deep and doubtless closed extremity, and at various parts they appeared to be implanted at some depth in the tissue of the uterus. Whether any of them divided into branches I could not determine. In a specimen belonging to Dr. John Reid, the uterus contained an early ovum, considered as dating little more than fifteen days after conception. The decidua vera was somewhat corrugated on the surface, it had the usual cribriform aspect, and the pits were for the most part wider than in the earlier examples ; but the smaller orifices still presented the character of the tubular glands, and others showed an obvious transition between these and the larger ones. On making a section parallel with the surface, it appeared that many of the pits had a comparatively wide cavity with a narrow orifice. From these and other observations of a similar kind I was led to conclude that the apertures on the decidua which give to that membrane its well known cribriform character, however much they may be modified in the later stages of pregnancy, are originally nothing else than the openings of the glands of the lining membrane of the uterus, and that, as in the bitch, the mucous membrane is really converted into the decidua, and discharged from the uterus at parturiton ; an opinion, it may be remarked, adopted on other grounds by various continental physiologists. In a uterus supposed to have been recently impregnated, and in which the vessels had been minutely injected with vermilion, the lining membrane or commencing decidua appeared everywhere pervaded by a network of blood-vessels, in the midst of which the tubular glands were seen, their white epithelium strongly contrasting with the surrounding redness. In more advanced stages the veins of the decidua form large ramifying canals in the substance of the membrane, which freely communicate with the uterine veins. On inflating these venous canals of the decidua with a blowpipe, the air will frequently pass out at the openings on the surface of the membrane which we have considered as the orifices of the enlarged uterine glands, and it might hence be concluded that there is a natural communication between the two. I am nevertheless disposed to think that the venous canals and glandular recesses form two separate systems of cavities within the decidua, divided from each other by very thin parietes which are easily ruptured. I am inclined to adopt this opinion in consequence of repeated examination, in various ways, of the structure with the borders of the carina of the embryo. In a drawing of a very young embryo, which has been sent to me by Professor E. H. Weber,

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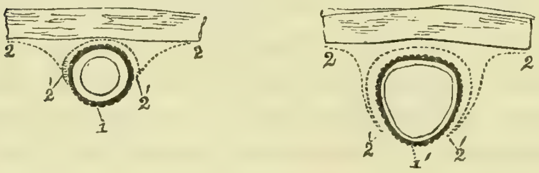
* Fig. 216. Two thin segments of human decidua after recent impregnation, viewed on a dark ground ; they show the openings on the surface of the membrane. A is magnified six diameters and B twelve diameters. At 1 the lining of epithelium is seen within the orifices, at 2 it has escaped.

in question (though I must admit that the result has not been always favourable), and also from considering that the pits in the decidua appear, as already stated, to be merely the enlarged uterine glands, which, when observed in earlier stages, seem to have the same relation to the surrounding blood-vessels of the decidua as is known to subsist between glands and blood-vessels in general.

An objection to the opinion that the decidua is merely the altered mucous membrane of the uterus which will naturally occur, is the difficulty of accounting on that view for the investment of the ovum by the decidua reflexa, which is continuous with the uterine decidua and is believed by most, though not by all physiologists, to have a similar origin. At the same time the force of this objection is lessened by the fact, that the decidua reflexa, though continuous with the vera, does not, usually, at least, present the same character as the vera throughout its whole extent; for, without laying stress on the differences generally pointed out by authors, I may state, that in various conceptions which I have examined the decidua reflexa in a great part of its surface was destitute of the small orifices which characterise the vera, and that these were confined chiefly, though certainly not entirely, to a zone of the membrane adjoining the angle of reflection, that is, to the part next the decidua vera. Now, if this observation be found to hold good generally, it will not be necessary to suppose that the lining membrane of the uterus is extended over the whole surface of the ovum to form the decidua reflexa; and although I am not prepared on such limited observation to offer a decided opinion, especially on a question of acknowledged difficulty as this is, still, as at least a possible explanation, it might be suggested, that the minute ovum on its entrance into the uterus is covered with exuded lymph (1 in diagram), either entirely or on that part of its surface which does not adhere to the inside of the uterus; that as the ovum enlarges, a circular fold (2′ 2′) of the altered mucous membrane (2) (decidua) is drawn up upon it, all round its adhering part, enveloping the ovum to a greater or less extent, and afterwards forming the cribriform zonular portion of the decidua reflexa, whilst the remaining thin smooth portion of the latter membrane, which is more distant from the line of reflection, and is destitute of apertures, is formed by an extension of the covering lymph (1′). Or perhaps the following more simple explanation might not be inadmissable; viz. that the minute ovum on reaching the uterus becomes imbedded in the substance of the then soft and pulpy mucous membrane, and that in its subsequent enlargement it carries along with it a covering of the membrane, which is expanded into the decidua reflexa.

Fig. 217.



Are the cells observed in the human decidua, by Dr. Montgomery, identical with the dilated uterine glands ? Dr. M. occasionally found them to contain " a milky or chylous fluid," but he does not describe them as opening on the inner surface of the membrane.

In acknowledging the kindness of my friend, Dr. John Reid, now Professor of Medicine in St. Andrews, in freely placing at my disposal some very valuable specimens in his collection, I deem it due also to that gentleman to state that he had previously observed the tubular structure of the mucous membrane of the uterus, and was led, by an examination of recently impregnated uteri, to infer that one of the earliest changes which occur after impregnation was an increased development of the tubular strucnot only the duct of the umbilical vesicle, but its blood-vessels also are seen.*

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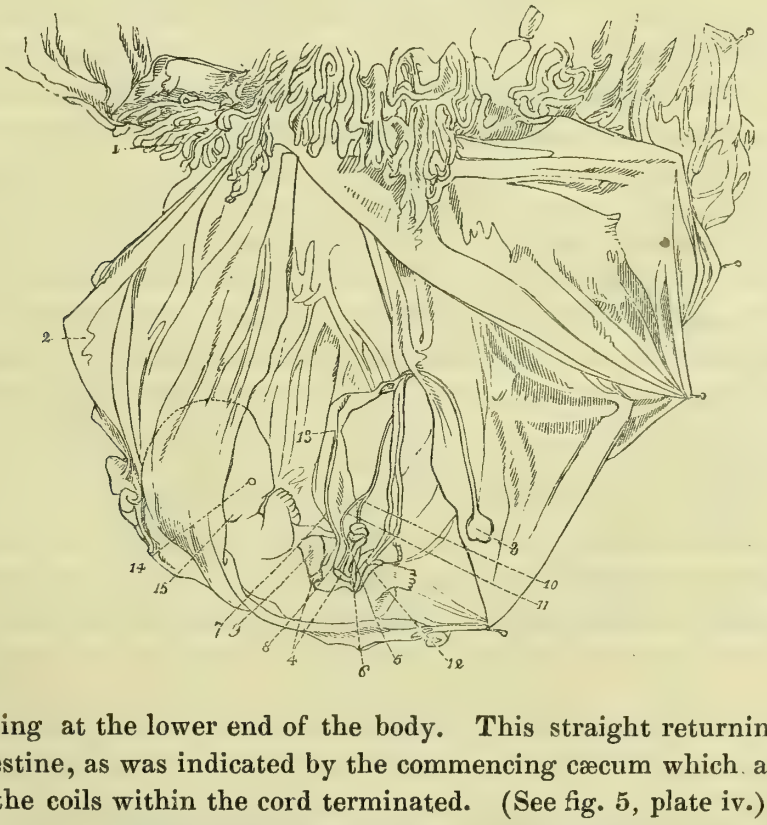
ture, and this he conceived was connected with the formation of the decidua: at the same time he did not suppose that the mucous membrane was converted into the decidua, but was disposed to think that the decidua was secreted by the tubes of the mucous membrane."]

* [The blood-vessels of the umbilical vesicle (omphalo-mesenteric vessels) are beautifully shown in the preparation of a human embryo belonging to Dr. Sharpey, who has allowed a drawing of the preparation (plate iii.) to be made for the use of this work. Figure 218 is an outline copy of the plate referred to. The aborted ovum measured about $1\frac{1}{2}$ inch. Abundant and large villi extended from the chorion (1) to the decidua at the part where the cord was attached. The amnion (2) is laid open, and the fœtus is seen lying at the bottom of its cavity. The extreme length of the fœtus was $1\frac{1}{20}$ of an inch; the length of the head from the vertex or highest point to the indentation beneath the jaw was $\frac{1}{2}$ an inch. The vesicular umbilicalis (3), rather more than $\frac{1}{10}$th of an inch in diameter, was left adhering to the outside of the amnion when the chorion was separated. The length of the pedicle from the vesicle itself to the point where it entered the umbilical cord was $\frac{7}{10}$ths of an inch. On laying open the abdomen of the fœtus and the cord, it was found that the intestine (4) on leaving the stomach made a turn to the right; then after a retrograde bend it passed through the umbilicus into the cord, at first straight (5), then making three coils in the cord, then returning straight again (6) into the abdomen, and terminating at the lower end of the body. This straight returning portion was the large intestine, as was indicated by the commencing cæcum which appeared at the point where the coils within the cord terminated. (See fig. 5, plate iv.) The umbilical vein (7) could be easily traced in the cord, and in the abdomen could be seen entering the lower part of the liver (9), being there connected with the intestinal vessels (vena porta ? 8). The umbilical arteries also (12) were easily seen. On tracing back the fine pedicle of the umbilical vesicle towards the fœtus, it was seen, on approaching the intestine, to consist of two filaments, which were separated by the coil of intestine. After a nice dissection, one of these (11) was traced back to the small intestine in the

Fig. 218.



In young ova the chorion is separated by a large interval from the amnion which at that period closely embraces the fœtus. The space is filled with a substance which is sometimes of a fluid consistence, at others gelatinous,—the "corps reticulé" of Velpeau (see fig. 224, page 1589). A thin layer of membrane (the Endochorion) may be readily separated from the inner surface of the chorion; so that the gelatinous or fluid body just described appears to be included in a special sac. Sometimes reticulated filaments traverse the gelatinous mass, being connected on the one hand with the endochorion, and on the other with the amnion. Many anatomists,—for example, Velpeau among the more recent writers,—have regarded this substance with its including membrane as the allantois of the human ovum, it being placed between the amnion, umbilical vesicle, and chorion, nearly in the same position as the allantois of Mammalia. This view has never been confirmed by observations on the development of the human allantois; and it is, moreover, in itself improbable. The "corps reticulé" appears to be a mere albuminous secretion; while the allantois very probably like the same part in the ovum of rodent animals, is developed merely as a narrow vesicle which elongates itself till it reaches the chorion, and is only destined

abdomen which it joined almost immediately below the stomach, enlarging somewhat at the point of its junction. This seems to be the omphalo-mesenteric vein. The other filament (10), also after a nice dissection, was found to proceed from the mesenteric vessels. These vessels appeared to arise by a thick tapering origin near the first turn of intestine which embraced them in its concavity; they then passed forwards to the part of the intestine contained in the cord, dividing into three or more chief branches, and from the middle one of these branches the second filament of the umbilical pedicle (the omphalo-mesenteric artery) proceeded. This origin of the omphalo-mesenteric artery displayed in fig. 5, plate iv. A part of the sheath of the cord is seen in plate iii. and in fig. 218 (13). The other anatomical facts observed in this fœtus were the following:—The eyeball (14) was surrounded by the circular border—the orbit—but was destitute of eyelids. The external ear (15) presented, faintly marked, the helix, antihelix, tragus, antitragus, and concha, but was scarcely elevated above the surface. There was no prominent nose. The nostrils were two round apertures less than $\frac{1}{20}$th inch apart, *from each of which a white line* extended downwards and a little outwards to the mouth,—a large transverse slit $\frac{2}{10}$ths of an inch long, and nearly on a level with the external ear. The limbs were distinctly divided into arm and fore-arm, thigh and leg; the fingers and toes appearing as rounded lobes at the broad edge which terminated the limb, while higher up they were separated by grooves.

In another, younger fœtus (measuring $\frac{6}{10}$ths of an inch in length) also dissected by and in the possession of Dr. Sharpey, the filament which appears to be identical with the omphalo-mesenteric vein has been traced further into the abdomen,—namely, beneath the intestine to the membrane, and probably to the vessels, which lie in the concavity of the first intestinal turn. This fœtus is represented in fig. 4, plate iv. The canal of the intestine has been cut transversely, and the minute filament or vessel is seen passing beneath it.

The above description of the embryos and corresponding figures is derived from Dr. Sharpey's notes.]

to conduct the umbilical vessels to that membrane. This view is supported by the observations of several embryologists,* who have seen two vesicles with narrow necks projecting from the abdomen of the early human embryo. (See fig. 220, page 1585.) The short and thick cord also which passed from the caudal part of the embryo to the chorion in the ovum, described some years since by myself,† appears to have been the allantois. (See figs. 1, 2, and 3, plate iv.) This cord was not composed of vessels, but appeared to be a simple structure. The same body is more distinctly seen in the ovum figured by Wagner.‡ (See fig. 222, page 1587.) In many cases the end of the allantois seems to dilate a little at the point where it is inserted into the chorion. Von Baer says that in all the ova of the first and second month which he has examined, he found a very small flattened vesicle at the point of attachment of the umbilical cord to the chorion, which communicated more or less distinctly with a duct contained in the cord. The vessels ran in contact with this duct which could be traced into the Cloaca.

Von Baer proposes two modes of explaining the connection of the allantois with the chorion. The vascular layer of the allantois may separate from the mucous layer and apply itself in the form of a distinct membrane to the external tunic of the ovum or the chorion; while the mucous layer remains in the form of a canal; in which case the albuminous mass found between the chorion and amnion would be a deposit between the vascular and the mucous layer of the allantois, such as takes place at a later period of development in the Solidungula. According to the other view, this separation of the layers of the allantois, does not take place; but the umbilical vessels extend from the small allantois, and implant themselves in the chorion; while the allantois itself undergoes no further development, and at length entirely disappears, leaving merely its pedicle—the urachus. If this were the process, the albuminous mass would be a deposit formed beneath the external tunic of the ovum; while that membrane assumed the character of the chorion. There are instances of the occurrence of both these processes in different mammiferous animals. Von Baer regards the latter as the more probable explanation; and I am myself of the same opinion, chiefly on the ground that Wharton Jones and Allen Thomson have observed the presence of the albuminous or reticulated mass in ova, where the embryo was not yet attached to the chorion, and the allantois consequently not developed. According to this view, the lamella lining the inner surface of the chorion would probably be the membrana serosa already described. (See page 1571.)

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* Pockels, Isis, 1825, Tab. xii. xiii. Coste, Embryog. Tab. iii. figs. 4 and 5. Seiller. Tab. x. Von Baer's Entwickelungs-geschichte. Tab. vi. figs. 15 and 17; and in Siebold's Journal, No. xiv. figs. 7 and 8. A. Thomson, Edinb. Med. and Surg. Journal, No. 140, fig. 3, plate iii.

† Müller's Archiv. 1834, p. 8; and 1836, p. 167.

‡ Icon. Physiol. Tab. viii. figs. 2 and 3.

When the embryo by means of its vessels has gained a vascular connection with the chorion, the allantois can no longer be discovered, the urachus of the urinary bladder,—a filament extending into the umbilical cord,—being its only remains.

The successive changes which the ovum undergoes may be referred to the following stages:—The first stage extends to the appearance of the embryo, elevating itself above the surface of the yolk-sac. The changes which occur during this period are the least known; but the villi of the chorion are at this time developed. This stage is illustrated by an observation of Mr. Wharton Jones.* The ovum which he describes had the size of a pea, and was stated to be aborted in the third or fourth week after impregnation, but may have become detached at a much earlier period. It lay imbedded in one side of the uterine decidua. One side of its external surface was smooth, the other beset with villi. The whole cavity of the chorion was filled with a gelatinous tissue, in which towards one end of the ovum a small round body,—the vesicular germinal membrane,—was embedded. The embryo was not yet visible.

In the second period the embryo becomes separated by a constriction from the yolk-sac, and the amnion and allantois are developed; but the embryo is not yet attached to the chorion by means of the latter membrane. Two ova, observed by Dr. Allen Thomson,† belong to this period. Both these ova were beset with villi of the chorion. One measured one-quarter of an inch, the other one-half of an inch in diameter. In the smaller one the yolk-sac or umbilical vesicle occupied the greater part of the cavity of the chorion, but did not entirely fill it, the space between them being occupied by a thin tenacious web of albuminous filaments. The embryo, one line in length, lay with its abdominal side nearly flat on the surface of the yolk-sac, with which it formed a common cavity.

In the second ovum (fig. 219) the cavity of the chorion was in proportion to the embryo very large, and was filled with the above-mentioned filamentous tissue. The embryo and yolk-sac were connected to the chorion by a part of this tissue which was more dense than the rest. The embryo was not attached to the yolk-sac by a narrow pedicle, but lay nearly flat upon it, its sides passing uninterruptedly into the parietes of the yolk-sac. In this embryo the dorsal laminæ were remarkably distinct, they not having united at this period. Neither allantois nor amnion was present.

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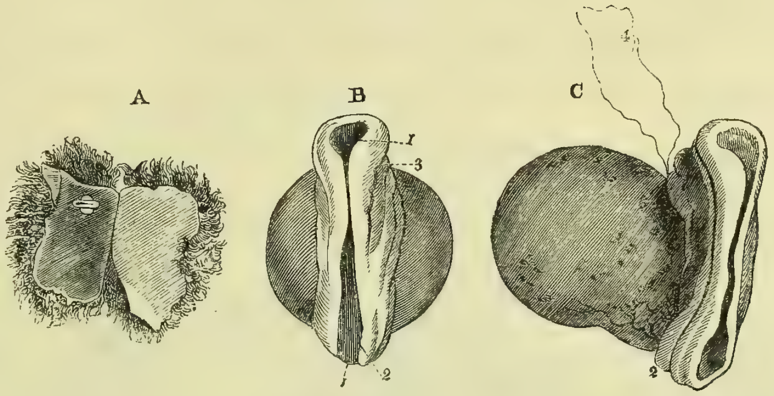
* Philos. Transact. 1837, p. 339. [See also an account of an early ovum observed by Volkmann, in Müller's Archiv. 1839, p. 248.]

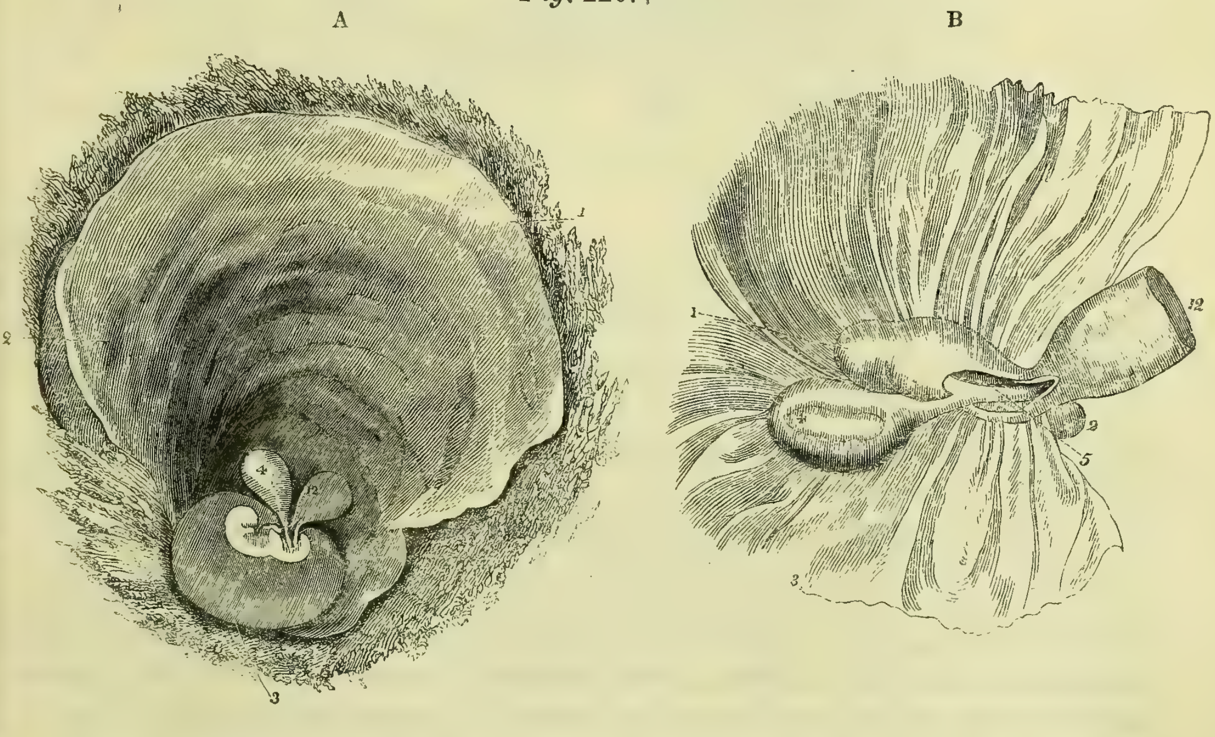
† Edinburg Med. and Surg. Journal, No. 140, figs. 1 and 2.

Fig. 219.*



To the same period are to be referred several ova in which the allantois has been observed in the progress of development. In these ova,—for example in those described by Pockels and Coste (see fig. 220),—two pedunculated vesicles project from the abdomen of the embryo, but neither is attached to the chorion.

Fig. 220.†



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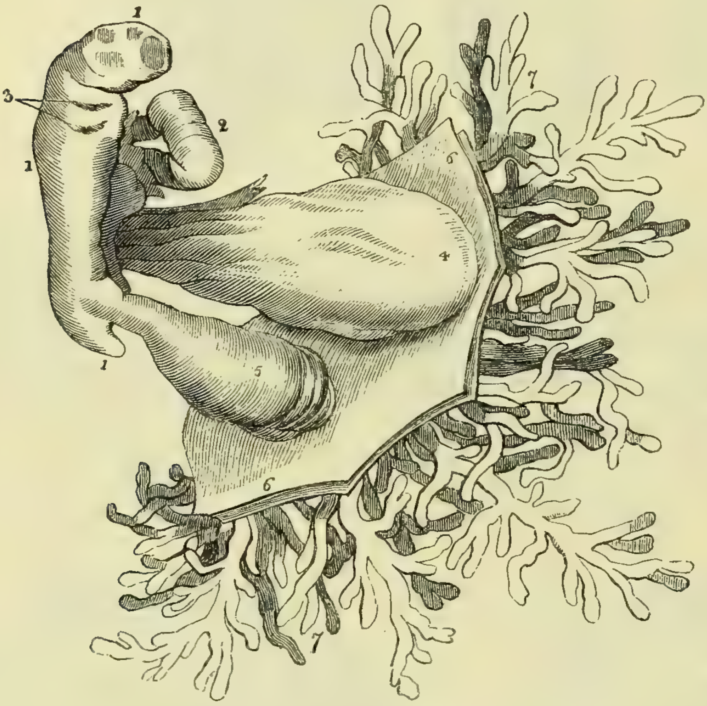
* [Fig. 219. The second ovum described by Dr. A. Thomson, and dating little more than fifteen days from conception. A, the cavity of the chorion laid open, showing in its upper part the yolk-sac with the embryo lying across it. B and C, the yolk-sac and embryo magnified ten diameters. The cephalic extremity of the embryo is uppermost: 1, indicates the open vertabral canal; 2, the folds of the intestinal groove; 3, the situation of the heart; 4, a piece of membrane which may be connected with the formation of the chorion.]

† [Fig. 220. A, An ovum belonging to a period between the 16th and 20th day, described and figured by Coste. "It is magnified to the extent of four diameters. The decidua, 1, and the chorion, 2, have been partially removed; and the embryo is dis-

A third stage of development extends from the period of the attachment of the ovum to the choroid by means of the allantois, to the complete formation of the umbilical cord. The amnion, however, has not yet formed a sheath to the umbilical cord, enclosing all the parts which issue from the abdomen of the embryo. This stage also is illustrated by an observation of Dr. Allen Thomson. The fœtus in this ovum (fig. 221) was $\frac{1}{8}$ of an inch in length. The heart hung from the anterior aspect of the body in the form of a looped vessel. The intestine was a straight canal, the mouth being present, but the anus not open. At the middle of the body the intestine opened by a wide orifice into the yolk-sac, or umbilical vesicle, which was beginning to become narrowed at its lower part. From the more posterior part of the fœtus a pear-shaped body projected, which attached it to the chorion. Two branchial clefts were visible. The amnion was not present (probably from the development of the ovum having been

Fig. 221.*



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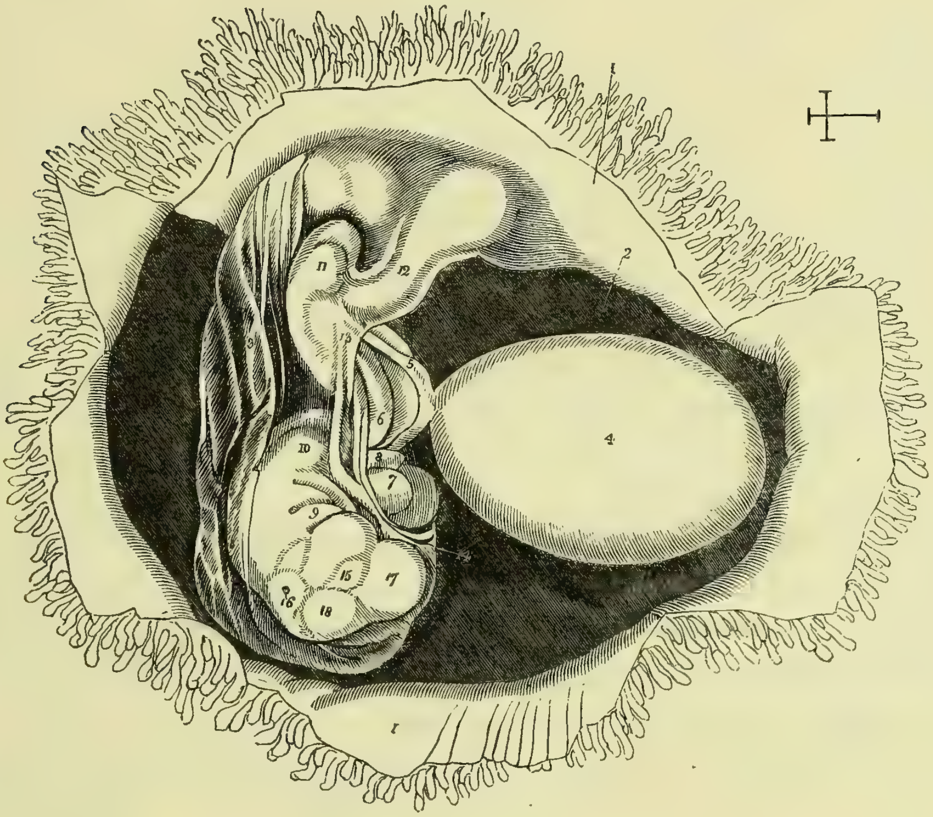
tinctly seen enveloped in the amnion, 3 ; the umbilical vesicle, 4, projects from the middle of the body ; and the allantois, 12, situated nearer to the posterior extremity of the embryo, is beginning to apply itself to the chorion. The pedicles of both enter the umbilical aperture, but are quite distinct from each other."

B. "The embryo from the same ovum magnified ten diameters. The cephalic extremity of the embryo, 1, is seen through the transparent amnion, 3 ; 2, is the caudal extremity of the embryo. The umbilical vesicle, 4, communicates directly with the intestinal tube, 5 ; and the allantois, 12, flattened at its extremity, by which it was in contact with the chorion, is continued laterally into the future abdominal parietes of the embryo ; whilst its middle part dips down into the pelvic cavity, where it communicates with the intestine."]

* [Fig. 221. The third embryo described by Dr. A. Thomson, and dating five or six weeks from conception. 1, 1, 1, indicate the head, body, and caudal extremity of the embryo ; 2, the heart in the form of a bent tube ; 3, two branchial slits ; 4, the umbilical vesicle or yolk-sac ; 5, the pyriform part, connecting the caudal extremity of the intestine and embryo with the chorion (6). The fœtus has been removed from the ovum along with the umbilical vesicle of a portion of the chorion, and represented magnified eighteen diameters.]

abnormally modified). Next in order to this ovum we must place two ova, precisely similar to each other, which have been observed, one by Wagner (fig. 222), and the other by myself. The latter is the one

Fig. 222.*



mentioned at page 1583. This ovum measured from seven to eight lines in diameter. It was sent to me by Dr. Wolff of Bonn. Figures 1, 2, and 3, Plate III. are copies of a drawing of the ovum and embryo, which Prof. D'Alton had some time since the kindness to make for me. The embryo is 2½ lines in length; the thick umbilical cord measures ⅔ of a line, and the umbilical vesicle 1½ line in diameter. The amnion is so closely applied to the embryo, as to be scarcely distinguishable with the naked eye. It is continued from the lamina abdominalis at the margin of the wide abdominal opening, and has become united with the whole length of the umbilical cord at its lower surface. The intestine is a canal occupying the cavity of the embryo, and opening directly by a very wide orifice into the umbilical vesicle, at the point where the abdominal lamina is reflected into the amnion; so that in the situation of the future duct of the umbilical vesicle there is merely a slight constriction. The cervical region of the embryo presents three pairs of branchial clefts and arches, behind which in the middle line, the tubular heart projects from the anterior face of the embryo. This ovum is particularly interesting from the time at which the coitus took place being accurately known. It was on the 2nd of December; at the next menstrual period, namely the 25th of December, the menses did not appear: on the 27th the coitus was repeated, and on the 5th of January abortion took place. If we were guided simply by these data, the age of the ovum must be either thirty-four or nine days. I regarded the latter view as improbable. (Von Baer and Wagner were incorrect in attributing to me the contrary opinion.) Von Baer conjectures that the ovum became separated during the second coitus, and, consequently, that it should be referred to the twenty-fifth day of development: Wagner is of the same opinion.

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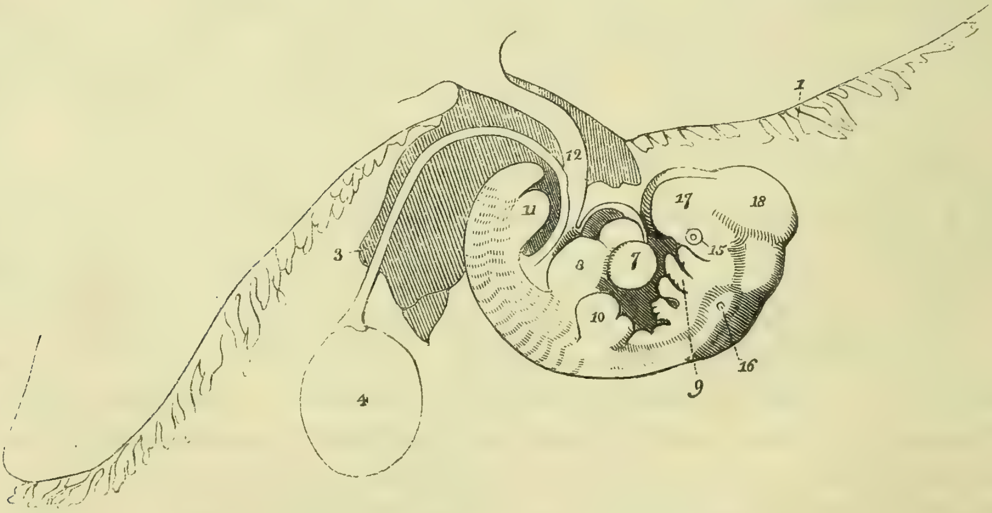
* [Fig. 222. The ovum and embryo described and figured by Wagner, and belonging to the third week (about the 21st day) from conception. The natural size of the embryo is shown at the side. 1. the chorion opened and reflected back; 2. the space between the chorion and amnion; 3. the amnion; 4. the umbilical vesicle or yolk-sac; 5. the intestine; 6. the corpus Wolffianum; 7. the heart; 8. the liver; 9. the inferior maxilla; 10. the anterior extremity; 11. the posterior extremity; 12. the allantois; 13. and 14. the points where the amnion is reflected back over the cephalic and the caudal extremities of the embryo; 15. the rudiment of the eye; 16. the ear; 17. the cerebral hemispheres; 18. the corpora quadrigemina.]

The ovum of three weeks' development, which is represented by Wagner (fig. 222) is in a very similar stage of formation. The rudiments of the extremities are just perceptible in the form of leaf-shaped projections. The different parts of the ovum are represented in so similar a state and form in the drawings of these two ova, that we seem to be justified in assuming them both to be in the normal condition.*

Fig. 223.



[* Figures 223 and 224 represent the human embryo at stages of development somewhat further advanced. Figure 223 shows an embryo of the fourth week, described and figured by Müller in Meckel's Archiv. 1830. The length of the embryo was 3½ lines. The ovum was open and the amnion torn, when it was obtained by Prof. Müller. 2. is the chorion; 3. a remaining part of the amnion, which was firmly attached to the chorion at the point of insertion of the umbilical cord; 4. the umbilical vesicle from which the long pedicle passed, enclosed in the

The space between the chorion and amnion filled with albumen exists only during the first and second months of pregnancy. In consequence of the growth of the amnion, the two membranes come into close relation with each other; although they are still separated by the tunica media, so accurately described by Bischoff.

The umbilical vesicle, which at first communicates with the intestine by a wide and short passage gradually, like the yolk-sac in birds, acquires a long and delicate pedicle, the "ductus omphalo-entericus," which is accompanied by the vasa omphalo-meseraica. This duct and the accompanying vessels then form part of the umbilical cord, the contents of which are held together by the reflected tube of the amnion, the "vagina funiculi umbilicalis." The umbilical vesicle, filled with a yellowish white yolk, is then found constantly lying between the chorion and amnion, at a varying distance from the insertion of the umbilical cord into the placenta. About the third month the vesicle, which has

umbilical cord, into the abdomen of the embryo ; 7. the heart ; 8. the liver ; 9. the visceral arch destined to form the lower jaw ; beneath which are two other visceral arches separated by the so-called branchial clefts : 10. is the rudiment of the upper extremity ; 11. that of the lower extremity. 12. is the umbilical cord ; 15. the eye ; 16. the ear ; 17. the cerebral hemispheres ; 18. the optic lobes or corpora quadrigemina.

Fig. 224.

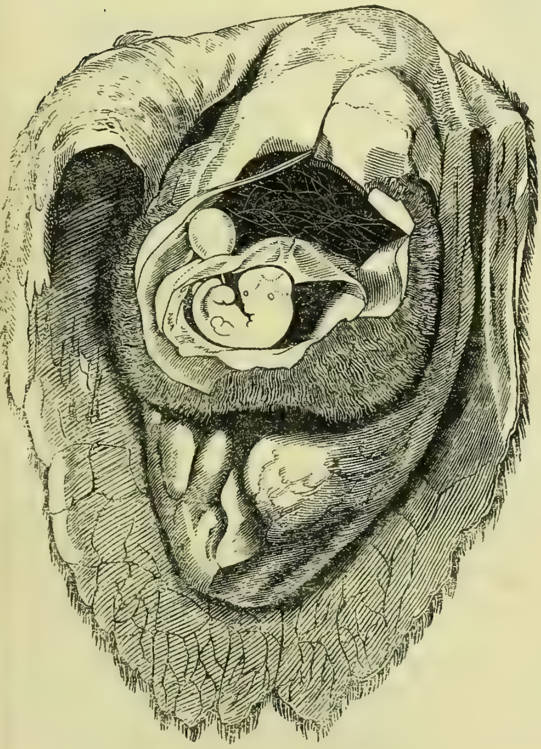


Fig. 225.

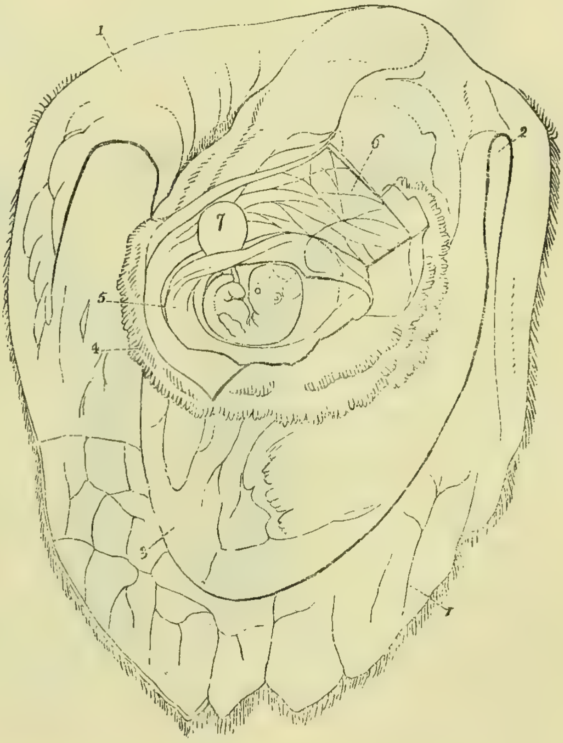


Fig. 224 represents an aborted ovum and embryo of five weeks, described and figured by Wagner, Icones Physiol. Tab. viii. Figs. v. and vi. The various parts of an ovum at this period are well seen, and all are in their normal state except the decidua reflexa. Fig. 225 the same in outline. 1. indicates the decidua vera reflected at 2, into the decidua reflexa (3.) which is thickened by the infiltration of blood ; 4. the villi of the chorion ; 5. the amnion laid open ; 6. the "corps-reticulé ;" 7. the umbilical vesicle.]

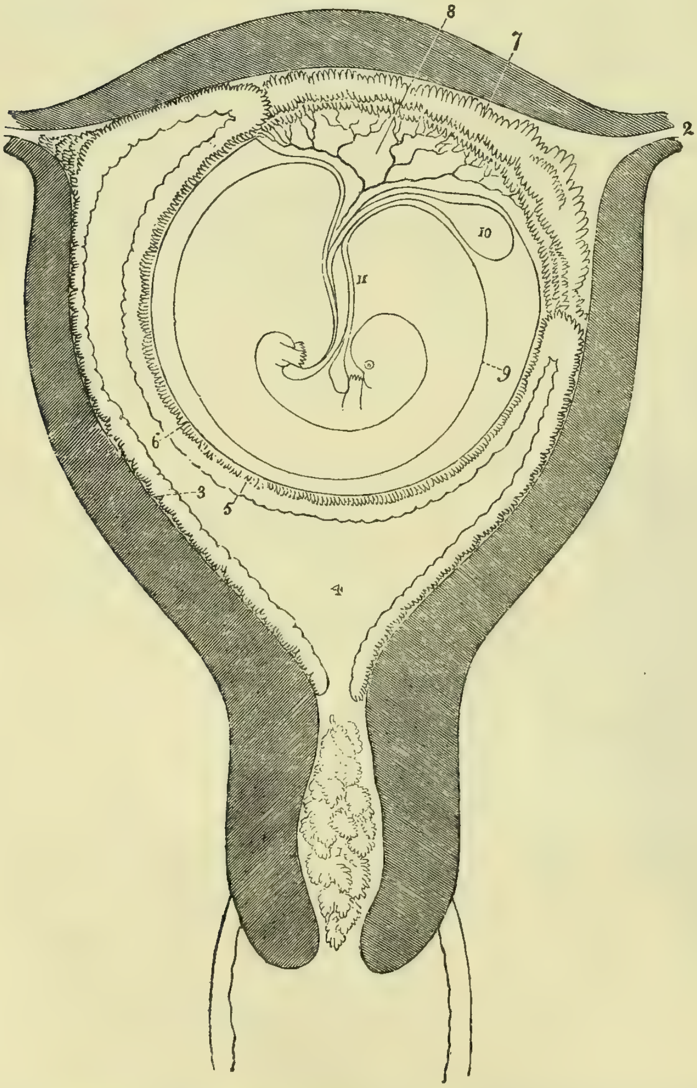
acquired the diameter of four or five lines, begins to become atrophied. The same is the case with its duct or pedicle. Sometimes, however, as Mayer has shown, both the vesicle and delicate thread-like pedicle can be detected even in ova of the full period of gestation.

When the Amnion and Chorion have come into close relation with each other, the ovum undergoes very little further change, except that the villi of the chorion become accumulated at one spot in order to the formation of the "placenta," and that the vessels of the chorion extend only at this spot into those branched processes or villi with clubbed extremities which, like the rest of the membrane, are composed of nucleated cells. The villi, however, do not disappear from the other parts of the chorion, but merely the interspaces between them become greater in consequence of the growth of the entire ovum. Even in ova of the full period these villi are still found upon the chorion.

During the development of the embryo the umbilical cord undergoes a constant increase in length.

In the fully formed ovum (fig. 226), the following membranes are found in passing from without inwards, closely applied to each other; first the decidua (3, 5), next the chorion (6), and last the amnion (9); the amnion being reflected upon the inner surface of the chorion at the point of insertion of the umbilical cord (11), of which it forms the sheath, while at the umbilicus it becomes continuous with the inte-

Fig. 226.*



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* [Represents a perpendicular section of a uterus with a fully formed ovum. A plug of lymph (1) occupies the cervix uteri; 2, indicates the opening of the Fallopian tube of one side; 3, the decidua vera; 4, the cavity of the uterus nearly filled by the ovum; 5, the decidua reflexa; 6, the chorion; 7, the decidua serotina (see page 1573); 8, the allantois and the situation of the future placenta; 9, the amnion; 10, the umbilical vesicle; 11, the umbilical cord. This diagram is copied from Wagner's "Icones Physiologicæ." Tab. vii. fig. x.]

gument of the embryo. The cord invested by this tubular sheath of the amnion, contains the following parts:

1. The remains of the ductus omphalo-entericus, or pedicle of the umbilical vesicle; accompanied by
2. The vasa omphalo-meseraica, branches of the mesenteric vessels of the fœtus;
3. The urachus; and,
4. The vasa umbilicalia, which in the later period of uterine gestation constitute the principal part of the umbilical cord. In mammiferous animals there are generally two umbilical veins as well as two arteries; but in the human subject there is but one umbilical vein and two umbilical arteries. The umbilical arteries are the main branches of the arteriæ hypogastricæ. They convey the blood of the fœtus into the placenta, or rather into the vessels of the aggregated villi of the chorion, which form the greater part of the placenta. In these villi, which are imbedded in the decidua of the uterus or the uterine placenta, the blood of the umbilical arteries passes through loop-shaped capillaries into small veins, which by their union form the vena umbilicalis. The vena umbilicalis, of which the persistent vena abdominalis of reptiles and amphibia is the analogue, pours its blood partly into the vena portæ and partly through the ductus venosus Arantii into the vena cava.

The *liquor amnii* of the human ovum contains, according to the analysis of C. Vogt,* an alcoholic extract with lactate of soda, chloride of sodium, albumen, and sulphate and phosphate of lime. The liquor amnii of an ovum of 3½ months' gestation had a specific gravity of 1·0182; that of an ovum of six months, a specific gravity of 1·0092. In the former 1000 parts contained 10·77 parts of albumen; in the latter only 6·67 parts.†

Having thus passed in review the general changes which the human ovum presents in the progress of its development, I proceed to the consideration of a question which has been hitherto only incidentally mentioned;—I mean the question,—what import should be attributed to the resemblances observed to subsist between the embryos of different classes of animals. Not long since it was supposed and seriously affirmed by many naturalists that the human embryo, previously to arriving at its perfect state, passed through the different stages of development which are permanent conditions of other animals. This was a very bold hypothesis, and one that is by no means correct. Its falsity was well demonstrated by Von Baer. The human embryo, in fact, at no period resembles a radiate animal, or an insect, a molluscous creature, or a worm. These animals are constructed after a plan which is totally different from that which regulates the formation of the vertebrata. Man, therefore, being a vertebrate animal, and being constructed according to the general type of the vertebrata, could at most, in the progress of his development, present resemblances to other vertebrate animals. But it is not true even that he resembles at one time a fish, at another time one of the amphibia or reptiles, and at another time a bird; he merely bears the same resemblance to a fish which he does to a bird or reptile, namely, the resemblance which all vertebrate animals bear to each other. In their first condition, the embryo of all these animals have in the highest degree the most general and simple characters of the type according to which they are formed, and hence at this period they all resemble each other so closely, that it is often difficult to distinguish them. At first, therefore, the fish, the reptile, the bird, the mammal, and man conform very closely to the common type, but in the progress of their development they gradually depart from it; the extremity, for example, which was at first the same in all, by degrees assumes the form of a fin, a wing, a paw, or a hand. Hence we may understand how it happens that all embryos have at first arches separated by clefts at the sides of their neck, the parts unaptly termed branchial arches; these being merely an expression of the general plan of structure, and having as yet none of the attributes of branchiæ. In all animals these arches contain branches of the aorta, which reunite posteriorly to form the descending aorta; but it is only in fishes that they undergo a progressive metamorphosis, consisting of the development of branchial laminæ upon some of the arches, and of the conversion of the aortic vascular arches into a system of blood-vessels with a pinnate arrangement, and distinct arterial and venous trunks; the latter of which unite to form the descending aorta. The same process takes place in the amphibia; but their branchiæ dwindle away at the time of the metamorphosis from the state of larvæ. The branchial vessels are reduced to the primary unbranched aortic arches; while their branchial arches for the most part disappear, and as happens at an earlier period in reptiles, birds, mammals, and man, are converted into other persistent structures. In the embryos of the latter animals the aortic arches also which are expressions of the common, simple type of the vertebrata, in greater part disappear, and there remain in the reptiles only two or at most four arches, and in birds, mammals, and man, only one.

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* Müller's Archiv. 1837, p. 69.

† For representations of ova belonging to the different periods of utero-gestation I refer to the works of Soemmering, Leiler, Velpeau, and R. Wagner.

The writings which treat on the same subject are those of Kieser, Pockels, Burdach, Leiler, Velpeau, Bischoff, Valentin, Mayer, Coste, Von Baer, Wagner, and Thompson, which have been already referred to; also Wrisberg's Descriptio Anatom. Embryonis, Gött. 1764; Autenrieth's Suppl. ad Hist. Embryon. Hum. Tub. 1797, and the paper by the author in Meckel's Archiv. 1830. p. 411.

The process of development of the human embryo will be described more minutely in the following section, in which the development of the different organs are treated of separately; but some of the principal changes in its form and size will be here recounted. *At the commencement of the second month* the length of the embryo extends to a few lines, or half an inch. The extremities are then visible in the form of leaf-like appendages, and the cavity of the mouth exists and is wide open; the anus is developed somewhat later; the coccyx is very prominent. The branchial clefts have not yet disappeared, though they soon afterwards become closed; the head acquires a considerable size; the eyes, which are at first placed laterally, assume a more anterior position, and the nasal cavities soon become developed. The attachment of the umbilical cord is yet very near to the posterior extremity of the trunk; but in the progress of development it moves more forwards, and at length occupies the middle point of the abdomen. *During the second month* the sheath of the umbilical cord is formed; the intestine, at first a straight canal, receives an angular bend with the apex of which the umbilical vesicle is connected, and this bent or loop-like part of the intestine is at this period received into the commencement of the vagina funiculi umbilicalis. (See fig. 4, Plate IV.) *Towards the end of the second month* ossification also commences at several points, and the rudiments of the muscular system are formed. The heart is covered in, and its septum begins to be developed; the aortic arches are reduced in number to two, which unite posteriorly to form the aorta descendens, and one of which subsequently becomes the pulmonary artery. The glandular viscera, the lungs, liver, and the Wolffian bodies exist. The formation of the last-named organs is soon followed by the development of the rudimentary kidneys, and the testes or ovaries. The external organs of generation make their appearance in the form of a wart-like prominence in front of the cleft which leads to the sinus urogenitalis. The urinary bladder is formed at a later period by a part of the sinus just named, leading in the direction of the urachus, being separated from the rest by a constriction. At this time the oral and nasal cavities are not separated; the eyelids and external ear, however, are beginning to be formed; the different parts of the extremities become perceptible, and the hands and feet present marks of the division into the digits. The embryo is now about one inch in length. *In the course of the third month* the fœtus acquires the length of two and a half or three inches; *in the fourth*, during which the sex becomes distinguishable, it reaches to four inches; and *in the fifth* to twelve inches. At this period occur the formation of the fat, and the further development of the rudimentary horny structures, the nails and the down, lanugo, which appears over the whole surface, and the eyelids coalesce. In the fifth month, also, the movements of the embryo are felt by the mother. A fœtus born during the *sixth month* breathes, but does not continue to live. In the *seventh lunar month* the embryo acquires the length of 16 inches or more, and if expelled from the uterus is sometimes capable of living; its skin is red. In the *eighth lunar month* its length is 16½ inches; the testes at this period descend from the abdominal cavity through the inguinal ring into the scrotum, which had hitherto the form of empty folds of skin; and the eyelids become free. In the *ninth month* the hair appears on the head, and the embryo measures 17 inches in length. In the *tenth lunar month* its length reaches 18 or 20 inches. At this period, or even during the eighth or ninth month, the membrana pupillaris disappears; and the skin, no longer so red, is covered by an unctuous matter, the "vernix caseosa," which, according to R. Wagner, consists of the desquamated scales of epidermis. In other animals the skin seems to throw off the epidermis in the form of a continuous membrane, and hence the body of the embryo has been frequently seen enveloped in this free epidermal membrane, whilst the hairs which had been formed subsequently were growing beneath it. [More recent observations on the developement of the human ovum and embryo, will be found in the Appendix.]

CHAPTER IV.

OF THE DIFFERENCES PRESENTED BY THE PROCESS OF DEVELOPMENT IN OVIPAROUS AND VIVIPAROUS ANIMALS.

The development of the ova of different animals takes place under very different conditions. Sometimes the ova are expelled from the system of the mother, and undergo development independently of it, the requisite nutriment being contained within themselves. Such is the case in oviparous animals. In other instances the ova are developed within the body of the mother, but yet lie free in the cavity of the uterus, with which they have no organic connection. Here also they derive for the most part no nutriment from without, although they may appropriate for their growth the fluid secreted by the uterus. I propose to apply the name of "Vivipara acotyledona" to all those viviparous animals, the ova of which are not connected with the uterus by means of vascular cotyledons or a placenta. The third class of animals are those in which such a connection with the uterus, destined for the assumption of nutriment, exists. These are "Vivipara cotylophora." In all these animals the ovum when it enters the uterus is very small, it not being necessary that it should contain a supply of nutriment within itself.

I. *Ovipara.*

The greater number of animals, invertebrate as well as vertebrate, are oviparous. The oviparous vertebrata comprehend the majority of fishes, reptiles, and birds. Few of the plagiostomatous fishes (the Sharks and Rays), however, are oviparous; namely, among the sharks only the family Scyllium, with seven genera, and amongst the rays only the family Raia. The ova of the oviparous sharks and rays, and of the Chimæræ, have a very firm horny shell of a flat form; and the gland destined for the formation of the shell is in these animals remarkably developed. One mammal, the Ornithorynchus, has been supposed to be oviparous; but, according to Mr. Owen, the correctness of this supposition is very much to be doubted.

The ova of oviparous animals, when deposited, in some cases undergo their further development in the water, in other cases on land. The development of the ova of fishes takes place invariably in the water, whilst among reptiles and Amphibia there are some of which the ova are developed in the water, others in which this is effected on land. The ova of Amphibia generally undergo the changes of development in the water, and their external investment, the analogue of the shell, imbibes the water so as to become greatly swollen. The ova of Alytes obstetricans, however, are developed in the ground, and the male sitting close to the female in the loose earth of a declivity bears the strings of ova wound around his feet. The ova of this animal have a hard horny shell, which is continued in the form of a thread from one ovum to another. In the Pipæ the ova, after they have been spread by the male over the back of the female and impregnated, are developed there, each in a cavity of the skin, which surrounds the ovum in the manner of a membrana decidua. The ova of several species of Syngnathus are developed in a furrow or groove at the surface of the abdomen or tail. The development of the ova is sometimes effected spontaneously, under the influence merely of the general conditions of nature, at other times, as in birds, with the aid of the parent which supplies the temperature required for the process.

II. *Vivipara Acotyledona.*

Very frequently the ova undergo complete or partial development in the oviducts of the parent animal. In the ova of Lacerta agilis the process has already advanced some extent at the time of their discharge. In Lacerta crocea the entire development of the embryo is completed in the oviduct. The poisonous serpents are viviparous, whilst the harmless species are oviparous. In both, the shells of the ova are of the same thickness; but in the former they are soft, in the latter hard, containing more calcareous matter. The true or land salamanders are viviparous; the tritons or water salamanders are oviparous. Amongst the osseous fishes the viviparous species,—such as Anableps and Zoarces,—are rare in comparison with the oviparous. Amongst the cartilaginous fishes the reverse is the case; for the Sharks and Rays are for the most part viviparous,—namely, the families Galei, Musteli, Zygænæ, Alopeciæ, Spinaces, Scymni, Squatinæ, &c. amongst the Sharks, and the families Pristides, Rhinobatides, Torpedines, Trygones, Myliobatides, and Cephalopteræ amongst the Rays. The coverings of the ovum in the viviparous Sharks and Rays are remarkably thin; and the ova increase in size by the absorption of a peculiar fluid secreted by the uterus; for Dr. J. Davy has observed that a developed embryo of the Torpedo is absolutely much heavier than an undeveloped ovum of the same animal. Before the appearance of the embryo the ovum of a Torpedo weighed 182 grains, and an ovum in which the embryo was visible weighed 177 grains, whilst the weight of a mature fœtus was 479 grains. This fact is important, since it shows how nearly allied are the viviparous generation without connection between the fœtus and uterus, and the form of viviparous generation in which that connection subsists.

Amongst the Mammalia also there are vivipara acolytophora,—that is, viviparous animals in which the ovum is not connected to the uterus by means of a placenta. Mr. Owen has given the following description of the embryo and membranes of the ovum of a Kangaroo, which had passed through half the usual period of gestation,—38 days. The membranes consisted of an amnion, a yolk-sac, and a very thin, non-vascular chorion. The allantois and placenta were wanting. In a uterine fœtus of a Kangaroo, the development of which was further advanced, and which has been described by M. Coste, as well as by Mr. Owen, the umbilical cord extended about three lines beyond the surface of the abdomen, the amnion forming a sheath for it. The cord then divided into two sacs. Of these sacs one, very vascular, was, like that seen in the former fœtus, the analogue of the yolk-sac, and was accompanied by the vasa omphalo-meseraica. The second sac had not more than one-sixth of the size of the one just described, was pear-shaped, presented numerous ramifications of the vasa umbilicalia, and formed a true allantois. This sac, however, had no connection with the uterus.*

The fœtus of the Kangaroo is expelled from the uterus at an extremely early period, when it measures scarcely more than an inch in length. It is then placed by the mother in the marsupial pouch, and applied to one of the nipples, attached to which and sucking, it passes through the further stages of its development. This natural premature birth is one extreme amongst the varieties of the process; the other extreme, a case of protracted birth, occurs in the Pupiparous insects, Hippoboscus, Melophaga, &c. which pass through their entire larval condition within the body of the parent, and are born in the state of Pupæ. A phenomenon somewhat analogous to this last mentioned is that presented by the Rana Pipa, in which the embryos are developed in cavities of the skin of the female, and do not escape thence until they have quite passed through the condition of larvæ.

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* See Owen, in Loudon's Magazine of Natural History. New Series, vol. i. p. 471. Coste, in Comptes Rendus, Fevr. 1838.

III. *Vivipara Cotylophora.*

A placenta exists only in the human subject, in Mammalia and in some genera of sharks. The connection between the fœtus and the mother usually consists in the very close contact of the corresponding surfaces of a placenta uterina and a placenta fœtalis; the vascular folds or villi of the latter being inserted in the manner of roots into depressions or cavities of the former. The placenta fœtalis is sometimes formed by the yolk-sac, namely in some Sharks. In this case the vessels which ramify in the fœtal placenta, and convey the nutritive materials from the uterine placenta to the fœtus, are the vasa omphalo-meseraica. Generally the placenta fœtalis is formed by the chorion, and its vessels are the vasa umbilicalia, which are conducted to the chorion by an allantois. This is the structure existing in those vivipara cotylophora which have an allantoid or vasa umbilicalia and vascular chorion, namely in the Mammalia and Man.

a. Connection of the fœtus with the uterus by means of a placenta in some genera of sharks.

Aristotle was acquainted with the remarkable varieties in the mode of development of the ovum presented by the Sharks. In the tenth chapter of the sixth Book of his Natural History, amongst many other observations worthy of consideration respecting the cartilaginous fishes, he says that there are both oviparous and viviparous sharks, and that in some of the latter the fœtus is connected to the uterus just as in Mammalia. The oviparous are the family Scyllium, whilst the Squalus, Vulpes, and Squalus acanthias are viviparous.

"But in those sharks which are smooth and are called ‘λεῖοι,’ the ova lie as in the Scyllium between the oviducts. When they separate from the ovary they enter each of the two oviducts, and the embryos are there developed, an umbilical cord connecting them with the walls of the uterine cavity; so that after the ovum (the yolk) is consumed, the embryo appears to have the same relation to the parent as in quadrupeds. A long umbilical cord is connected to the lower part of the uterus by means of a body like a placenta, whilst at its other extremity it is attached to the embryo about the middle, where the liver lies."*

The term Galeus lævis has been fixed as applicable to a particular species of shark by the ichthyologists of the sixteenth century,—Belon, Salviani, and Rondelet. Salviani and Rondelet, contemporaneous but independent writers, both regarded the shark with ray's teeth, the

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* Aristotle, Hist. Animal. vi. p. 10. See also De Generat. Anim. ii. p. 3.

Squalus mustelus of Linnæus, as the γαλεὸς λεῖος of Aristotle ; and Rondelet represents that shark with an umbilical cord passing from the sexual orifice of the mother to the navel of the young fish. Fabricius, Tyson, Collins, and Camper observed the embryo of a shark which they called Galeus lævis; but it is doubtful whether this was the shark with teeth like those of the ray. Here no connection of the fœtus to the uterus by means of a placenta was observed ; but, on the contrary, there was attached to the navel merely the simple yolk-sac,—as in the oviparous, and the other viviparous, sharks. At that period Galeus lævis was a term applied to any shark which was not rough, and more especially to any which had no spines on the dorsal fins. Cavolini associates the Squalus mustelus of Linnæus (or the shark with teeth like those of the ray), the embryo of which he had seen, with the γαλεὸς λεῖος of Aristotle. When speaking, however, of the generation of the cartilaginous fishes, he does not allude to Aristotle's observation.

On the other hand some facts have been accidentally observed which, although they were not originally adduced in confirmation of the assertions of Aristotle, yet agree therewith. Stenonis* described the embryo of Galeus lævis or Pesce palombo, which was connected with the uterus by means of a placenta. The placenta was hollow, and its cavity communicated with the valvular intestine of the fœtus through the medium of a tubular canal contained in the umbilical cord. This fish was not so described that its identity could be determined; all that is known of it being that it had an intestine with a spiral valve.

Dutertre † described a Requiem shark which, according to the description and drawing of it given by him, must have been a Carcharias. Dutertre says that its young were fixed by means of a cord to a large membrane. Cuvier‡ also says briefly in his great work on fishes that in the Carcharias the yolk-sac is attached to the uterus as firmly as a placenta. "Toutefois le vitellus fort réduit des fétus des requins prêts à naître m'a paru adhérer à la matrice presque aussi fixément qu'un placenta." The yolk-sac of this fœtus was also beset with villi. Neither Stenonis, nor Dutertre, nor Cuvier refers to the old observations on this subject.

The fish examined by Cuvier was of the genus Carcharias, but not the Carcharias with saw-like teeth (Prionodon of Müller and Henle); for in the latter species the interior of the yolk-duct is destitute of villi and quite smooth. This villous structure, however, exists in the subgenus Scoliodon of Müller and Henle. But the Carcharias, with saw-like teeth, in which the yolk-duct is devoid of villi, has, according to my observations, as well as the Scoliodon, that connection with the uterus by means of a placenta, which Aristotle discovered.

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* Act. Med. Hafn. Bartholini, 1673, vol. ii ; Hafn. 1675, p. 219.

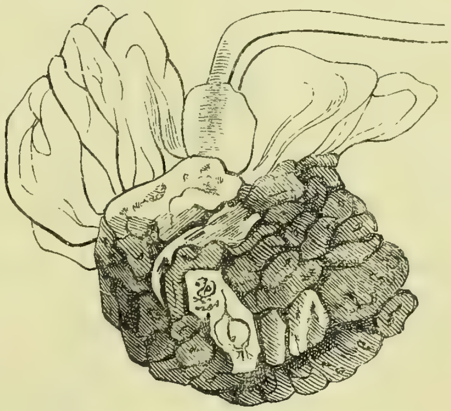
† Histoire des Antilles.

‡ Hist. des Poissons, T. i. p. 341.

The Galeus lævis of Stenonis does not belong to the genus Carcharias. It has an intestine with a spiral valve, as described and represented by Stenonis. But all the species of Carcharias have an intestine with a straight though waving valve. New researches have shown that two species of the genus Mustelus, with teeth like the rays, differ physiologically from each other in the circumstance that in one the fœtus, as in the genus Carcharias, is firmly connected to the uterus by means of a placenta, whilst the other has a yolk-sac which is quite free and unattached. The former, Mustelus lævis, (as Aristotle would have called it,) is distinguished by the narrowness of its thoracic fins, the form of its teeth, the position of the first dorsal fin behind the thoracic fins, and a dark spot passing through the posterior border of the tail. Of the second species, Mustelus vulgaris, there is a white-spotted variety and one destitute of spots, which in colour does not differ from Mustelus lævis.*

The placenta fœtalis of these fishes is formed by a plicated yolk-sac. The folds of the placenta are much more complex in Carcharias than in Mustelus lævis; and in the former genus the free portion of the yolk-sac forms several cœcal diverticula. The sharks of the genus Carcharias are also to be distinguished from the Mustelus lævis by the anatomical peculiarity of the trunks of the blood-vessels entering the interior of the yolk-sac before they are distributed in the folds.

Fig. 227.



In Carcharias the yolk-sac (fig. 227), as usual, possesses two coats, an internal vascular coat which is continuous with the intestine, through the medium of the yolk-duct, and an external non-vascular coat, which extends as a sheath over the yolk-duct and the omphalo-meseraic vessels, and is continuous with the skin of the fœtus at the anterior part of the abdomen, the ordinary point of insertion of the umbilical cord in fishes. For the formation of the placenta fœtalis both membranes of the yolk-sac are thrown into a mass of folds of different sizes. The interior of the yolk-sac is thus converted into a very irregular cavity with a large number of recesses. These wrinkled folds, at the side corresponding to the uterus, are most closely connected with that organ, and cannot be separated from it without some force. The part of the yolk-sac which is turned from the uterus presents merely freely floating diverticula (see fig. 227). As far as the yolk-sac enters into the formation of the placenta its two membranes are in the closest contact with each other; but at that part of it which forms the free and hollow diverticula, the membranes are separated from each other by a distinct interval. Both membranes, however, are closed at all parts.

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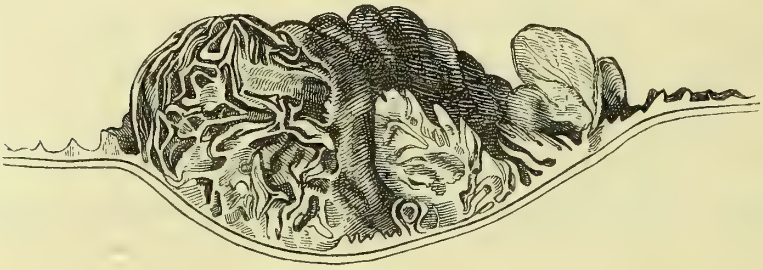
* See the Monats-bericht der Akad. der Wissensch. zu Berlin, 6 Aug. 1840.

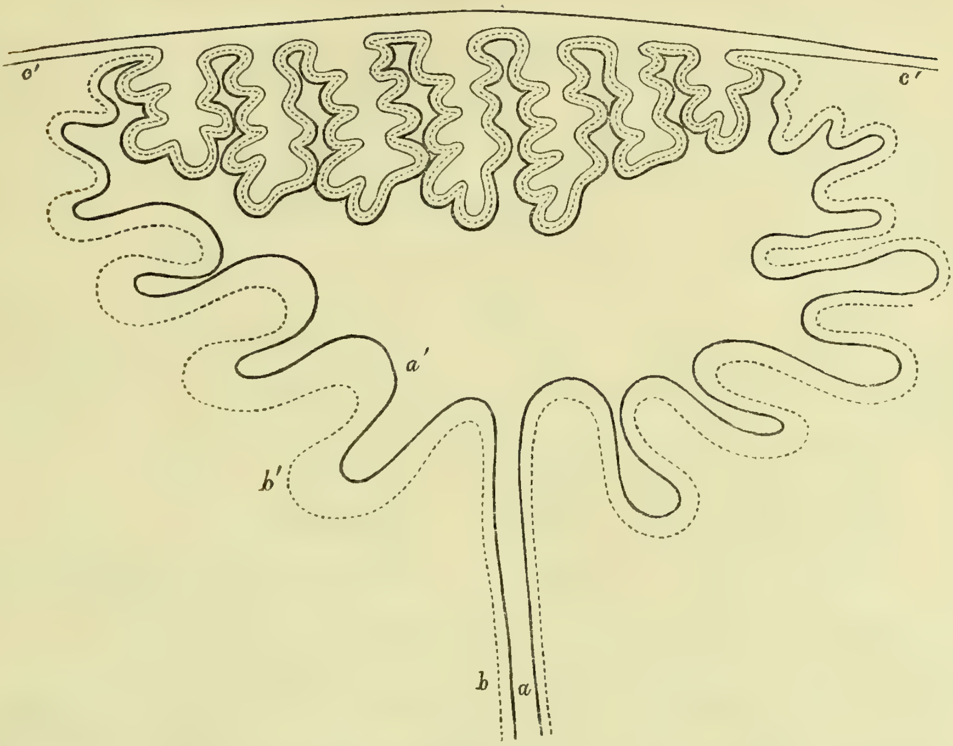
The placenta uterina (fig. 228) is constituted by very prominent wrinkled folds of the inner membrane of the uterus, which accurately correspond to those of the placenta fœtalis. The folds of both are interposed between each other, and are as closely and firmly attached as are the placenta uterina and placenta fœtalis of any mammiferous animal. The extremely delicate and structureless external membrane of the ovum passes between the folds of the two placentæ at the line where they meet, but where they are actually in contact seems to be dissolved; for when the two placentæ are forcibly separated the membrane in question cannot be detected, although by slowly and carefully withdrawing the numerous and very complex folds of the placenta from one another, the fœtal and maternal portions can be separated without suffering any injury. The following figure (fig. 229) represents an ideal but much simplified section of the organ. *a* indicates the yolk-duct; *b* the sheath of the umbilical cord; *a′* the internal membrane of the yolk-sac; *b′* its external membrane; and *c′* the internal coat of the uterus, which forms the placenta uterina.

Fig. 228.



The placentæ uterinæ receive their blood-vessels from the vessels of the uterus, which are of large size, and run to the seat of the placentæ at the lower part of the organ. The vessels of the placenta fœtalis are the extraordinarily large vasa omphalo-meseraica, which are here proportionally of as great size as the vasa umbilicalia of mammalia. The trunks of these vessels lie with the vitelline or yolk-duct in the sheath of the umbilical cord; but when they reach the yolk-sac they penetrate into the interior of the proper yolk-sac or internal membrane of the hollow placenta fœtalis, projecting nearly into the middle of its cavity, and are

Fig. 229.



thence distributed in a number of branches to the membrane of the yolk-sac, its folds, and diverticula.*

The minute structure of the placenta fœtalis and that of the placenta uterina are the same. The most external layer of the placenta uterina, which lies in immediate contact with the placenta fœtalis, consists like the decidua of the human uterus of microscopic nucleated cells. The substance of the membranes of the yolk-sac, the more external of which is destitute of vessels, has the same structure.

The organic relation of the placenta fœtalis and the placenta uterina to one another is the same here as in Mammalia. They lie in immediate contact, and this contact subsists over an immense surface of folds; but the vascular system of the parent is restricted to the uterine placenta, that of the fœtus to the placenta fœtalis. The organic attraction of matters from the maternal blood is probably effected by means of the microscopic cells.

The fœtus continues thus united to the uterus in the Carcharias and Scoliodon until it is fully developed. These vivipara cotylophora amongst the plagiostomatous fishes have the peculiarity of not possessing the internal vitelline sac within their abdomen. There are no vivipara cotylophora amongst the rays. The true rays (Raia) are oviparous, and all the other allied genera are vivipara acotyledona.

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* The vitelline duct is inserted into the intestine, as in the other sharks and rays, which have merely a simple yolk-sac at the upper extremity of the valvular gut, where the hepatic and pancreatic ducts likewise open into the canal. This upper end of the valvular gut is destitute of valvulæ, and is the part called by Ente the "bursa," and by Collins the "bursa Entiana," while more recent writers, not considering that Ente had not examined a fœtal shark, have applied the name of "bursa Entiana" to the internal yolk-sac, or even to the external yolk-sac of the Sharks.

b. Connection of the fœtus with the uterus in Mammalia and Man.[*]

The ovum appears to have a firm connection with the uterus in all Mammalia, with the exception of the Marsupialia and Monotremata. The means of attachment are always either vascular villi or folds of the chorion, and the chorion receives its blood-vessels from the vasa umbilicalia of the fœtus, which are distributed upon the allantois, and by it are conducted to the chorion. The villi are sometimes distributed over the whole surface of the chorion, as in the Hog family, the Solidungala, the Camel family, and the Cetacea; sometimes they form a zone around the ovum, as in Carnivora; at other times they are collected into several masses scattered over the chorion, the cotyledons, as in most Ruminantia; and lastly, in man and some other animals they form a single placenta upon one side of the chorion. The double placenta sometimes observed in the Rodentia approaches closely to the last form. Corresponding to the vascular villi of the fœtal chorion and placenta there are depressions upon the inner surface of the uterus in which the villi are imbedded like roots in the soil. When the villi are aggregated together at particular points of the chorion so as to form cotyledons, the uterus has at corresponding points maternal cotyledons,—projecting cup-like bodies, pierced by innumerable tubular cavities, which receive the villi of the fœtal cotyledons. In the human subject the placenta uterina is a growth of the decidua uterina, which at the part corresponding to the fœtal placenta undergoes an excessive development, and penetrates the substance of the fœtal placenta, passing between the tufts of villi even as far as the chorion. In all cases, whether the villi are scattered over a wide surface, or aggregated into masses, the object attained is a great increase of the surface of contact between the chorion and the uterus. Two principal modifications of the form in which this increase of surface is given, are to be observed, namely, the development of ramified villi imbedded in the uterus, and the formation of folds on both chorion and uterus, which are interposed between each other.

The varieties of structure will now be examined more in detail with relation to the different orders of animals.

In the Pachydermata, the placenta extends over the whole surface of the chorion, with the exception of the appendages of the ovum, and the chorion is uniformly beset with vascular villi. The placenta uterina in like manner extends over the inner surface of the uterus, which assumes a cellular structure, containing innumerable depressions or excavations for the reception of the villi of the chorion. A slight approach to the formation of distinct masses of villi is here presented by the less numerous larger depressions of the uterus, through which glandular tubuli open, and the corresponding circles of villi upon the ovum, which Von Baer has observed. The surface of the chorion in the dolphin is, according to Eschricht's researches, covered with rugæ and villi. The latter are separate from each other about the distance of half a line; they have not the form of folds as in the hog, nor of feathery cones as in the ox, but constitute numerous branched cauliflower-like round masses seated upon narrow pedicles. Hence the crowns of these villi are closer to each other than their bases. Their size varies; the largest measure about a line in length, and at their crown about one-fourth of a line in diameter. The crowns of these villi present an extremely beautiful net-work of capillaries. The inner surface of the uterus, likewise, has rugæ and also cells, which form sheaths for the villi. The walls of these cells are covered with capillary vessels. The Cetacea also have, like the Pachydermata and Ruminantia, uterine glands which secrete the fluid destined for the nutrition of the fœtus.

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[*] Writings on the subject. Von Baer, Untersuchungen über die Gefässverbindung zwischen Mutter und Frucht in den Säugethieren. Leipz. 1828. E. H. Weber in Hildebrandt's Anatomie, Bd. iv. p. 496, in Froriep's Notiz. 1835, Bd. 46, p. 90. and in Wagner's Physiologie, p. 124. Eschricht, de organis, quæ respirationi et nutritioni fœtus animalium inserviunt. Hafniæ, 1837.

In the Carnivora the placenta forms a zone around the ovum. The placenta of the cat has been shown by Eschricht to be formed of very thin laminæ, rising perpendicularly from the chorion, and plicated and disposed in an irregular manner. When the placenta is injected from the parent and from the fœtus with different coloured matters, the inner surface of the placenta appears completely variegated. On more accurate examination, it is found that this appearance arises from the intermingling of the laminæ of the chorion and those of the uterus, while the capillaries of one set of folds enter into no communication with those of the other. The laminæ reach through the entire thickness of the placenta, being two lines in depth; whilst they are extremely thin, their diameter not much exceeding that of blood corpuscules. At each margin of the lamina is a vessel of larger size than the capillaries of the general network. Eschricht shows that the uterine portion of the placenta of the cat is a vascular membrane, quite distinct from the mucous membrane of the uterus. For when it was removed, together with the fœtal portion of the placenta, the mucous membrane remained quite entire beneath, the blood-vessels only appearing torn. [See the observations of Dr. Sharpey on the placenta of the bitch at page 1575.]

The Ruminantia are divisible into two classes in respect of the structure of the placenta. In one which embraces the camel and lama, the chorion is universally beset with numerous scattered villi. In the other class, comprehending the giraffe, according to Mr. Owen, as well as the ox, sheep, goat, stag, &c. the villi are collected together so as to form cotyledons, which are distributed over the chorion, whilst the surface between them is destitute of villi. Each cotyledon consists of numerous tufts of ramified vascular villi. The cotyledo uterinus, which is here persistent even in the intervals of pregnancy, forms a prominence on the inner surface of the uterus, and has sometimes the shape of a sort of cup, with thick prominent borders, as in the sheep; sometimes that of a slightly elevated rounded mass, with a contracted basis. On the surface of the cotyledo uterinus are seen the openings of the canals, which correspond to the tufts of villi of the fœtal cotyledon, and the walls of which are covered by a very close network of capillaries belonging to the maternal system.

The ovum of the sloth also has separate lobular cotyledons, but they lie near each other at one part of the chorion.* In the Rodentia and Insectivora the placenta has a concentrated form. The Rodentia have frequently two placentæ lying near each other, frequently also only one. The ovum of the rabbit, except in the situation of the placenta, is smooth and free from villi. Even where it is thus smooth it is provided with blood-vessels; but these, according to Von Baer, are not branches of the umbilical vessels which go to form the placenta, but are derived from the vasa omphalo-meseraica, it being the yolk-sac, and not the allantois, which extends over the greater part of the ovum. The allantois of the rat was observed by Eschricht to be thrown into a labyrinth of folds in the situation of the placenta. The placenta itself is composed of laminæ of the chorion and uterus, interposed between each other. In the mole, Eschricht was able to separate the fœtal from the uterine portion at the margin of the round placenta, and found the former composed of villi, the latter perforated with canals. In the apes also the placenta is single, and in this respect, as well as in the small size of the umbilical vesicle, these animals resemble man; but they are distinguished by having two umbilical veins. (Such is the structure in Cebus, Mycetes, and Hapale, according to Rudolphi.)

The human placenta is throughout composed of two elements, the parts of the placenta fœtalis and those of the placenta uterina intermingled. The fœtal placenta consists entirely of dense tufts of branched vascular villi, whilst the uterine placenta is formed of the substance of the decidua, which penetrates between the villi of the fœtal placenta even to the surface of the chorion, and completely encloses them. The exact relation which the two parts bear to each other is, however, according to Professor E. H. Weber, very different in man and in Mammalia. In Mammalia the vascular villi of the fœtus are received into the vascular sheaths of the uterine placenta, so that the capillaries of the fœtal and those of the maternal system come into contact with each other, and suffer an interchange of the matters which they contain. In the human subject, on the contrary, the vascular villi of the fœtus dip into wide blood-vessels, which arise from the uterine system, and which permeate the whole uterine portion of the placenta; the looped capillaries of the fœtus being thus surrounded and bathed, as it were, in the maternal blood. The ends of the villi are formed by the inosculating loops of the minute arteries and veins of the fœtus; which, however, have the distinguishing character that the same vessel makes several turns from one loop into another before it enters the nearest venous trunk. (See figs. 230 and 231.) The vessels belonging to the maternal system, which penetrate the uterine portion of the decidua and in all parts contain villi of the fœtal portion, may be readily filled with injection from the arteries of the uterus. Eschricht inclines to the

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* Rudolphi, Abhandl. der Akademie zu Berlin. J. 1828. The urachus of the sloth does not open at the fundus but near the neck of the urinary bladder.

Fig. 230.*

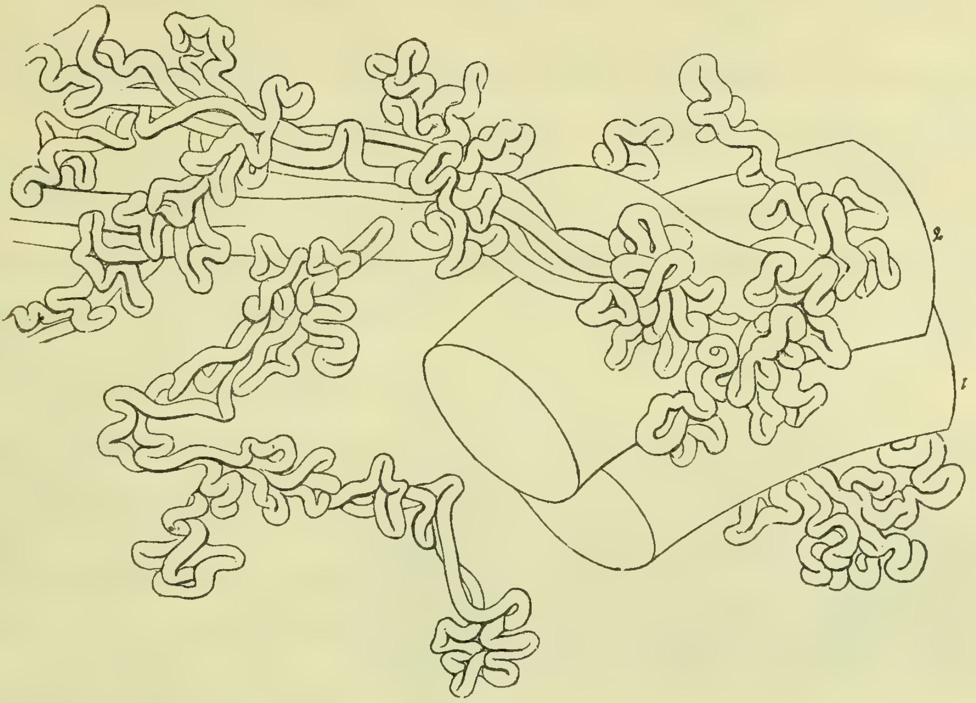
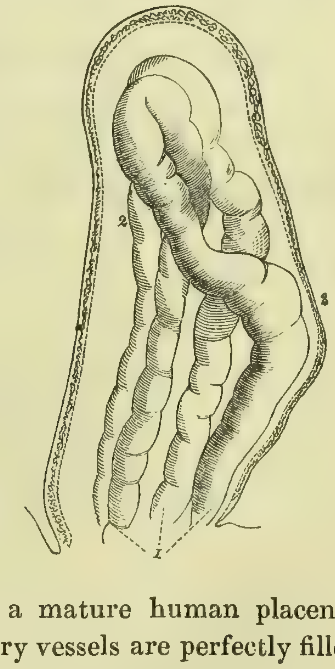


Fig. 231.†



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* [Fig. 230 represents the villi of the fœtal portion of a mature human placenta magnified 100 diameters; after E. H. Weber. The capillary vessels are perfectly filled with injection, and their diameter varies from $\frac{1}{115}$ to $\frac{1}{170}$ of a French line. 1, the artery: 2, the vein.]

† [Fig. 231 is the extremity of a villus; taken from a recent placenta, in which the vessels were still filled with blood, magnified 200 diameters; after Weber. The loop, 1, is filled with blood; the other loop, 2, is empty; 3, is the margin of the pellucid villus.]

opinion, that in man as in Mammalia, only the capillaries of the decidua come into contact with the looped vessels of the villi. Weber, on the contrary, maintains that the uterine arteries and veins on entering the spongy substance of the placenta, no longer ramify and give off branches and twigs, but take the form of a net-work, the canals of which are much larger than the ordinary capillaries. The extremely thin parietes of these canals, according to Weber, apply themselves to all the branches and capillary loops of the vessels which form the fœtal villi, so that even here the structure consists essentially in two sets of vessels being brought into the closest possible contact.*

[The recent observations of Dr. J. Reid (Edinb. Med. and Surg. Journ. No. 146,) agree in the most important points with those of Weber, but yet differ from them in some particulars. Dr. Reid's views are illustrated by figures 232, 233, and 234. According to Dr. Reid, the blood sent from the mother to the placenta is poured by the curling arteries of the uterus (1, fig. 232 and fig. 233), "into a large sac (3, fig. 233), formed by the inner coat of the vascular system of the mother, which is intersected in many thousand different directions by the placental tufts (3, fig. 232), projecting into it like fringes, and pushing its thin wall before them in the form of sheaths, which closely envelope both the trunk and each individual branch composing these trunks (fig. 233). From this sac the maternal blood is returned by the utero-placental veins (2, fig. 233) without having been extravasated, or without having left her own system of vessels." The uterine vessels, therefore, according to Dr. Reid, do not form a network in the substance of the placenta as de-

Fig. 232.

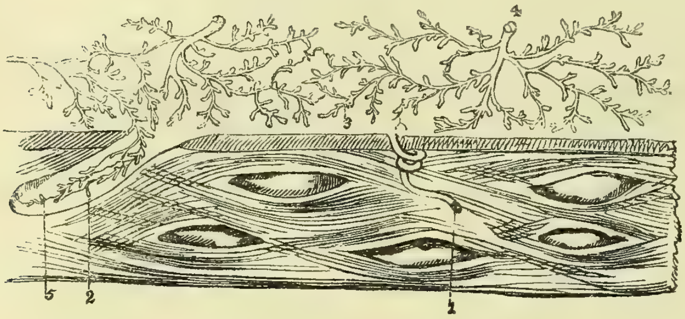

Fig. 233.

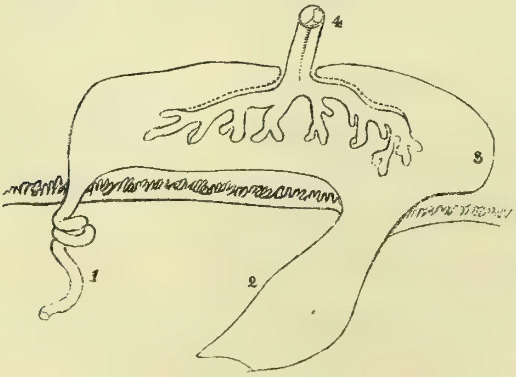

Fig. 234.

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* See the account of Weber's more recent researches in connection with this subject in Wagner's Physiologie, p. 124.

scribed by Weber. Further, Dr. Reid has observed, that the tufts of the placental vessels are prolonged into some of the uterine sinuses (2 and 5, fig. 232), a fact not noticed by Weber. Dr. Reid states also, that in the placental tufts each branch of the umbilical artery is bound up with a branch of one of the umbilical veins, and that both of them divide and subdivide exactly in the same manner, and terminate by inosculation with each other at the blunt extremities of the branched tufts. (Fig. 234; where 1 is the arterial, and 2 the venous twig.) It appears, however, that this description of the structure of the placental tufts is erroneous. In a paper on the structure of the placenta, recently sent in to the Royal Medico-chirurgical Society by Mr. Dalrymple, most satisfactory confirmation is given to Weber's account of the mode of termination of the fœtal vessels in the placental tufts. Several drawings, made by Mr. Dalrymple before he had seen the figures given by Weber in Wagner's Icones, (and copied at page 1605, figs. 230 and 231,) bear the most remarkable resemblance to those figures. The minute arteries and veins are not bound up together, two and two; but the same capillary tube, arising from an arterial trunk, makes several convolutions and forms several loops before it terminates in a vein.]

In the human subject, as in Mammalia, there is no passage of blood from the vessels of the mother into those of the fœtus, and *vice versâ.* When the placenta is injected from the vessels of the mother, as can be readily done, only the vessels of the maternal portion of the placenta are filled. And, on the other hand, the passage of injected matters from the umbilical arteries, or vein of the fœtus, into the vessels of the uterus, by no means proves the existence of a communication between the two sets of vessels; for the injected mass, becoming extravasated from the vascular loops of the fœtal placenta, must pass directly into maternal vessels, and if forced onwards necessarily fills the veins of the uterus.

The placenta fœtalis and the placenta uterina can be separated in some animals with great ease, and without injury to either; but in other animals and man they cannot be detached from each other without laceration. Von Baer remarks that the fœtal cotyledons of the Ruminantia, when they are only slightly developed, adhere so firmly to the maternal cotyledons which form sheaths for the villi, that it is impossible in their fresh state to withdraw them uninjured. But after a short period has elapsed they are easily separable, and then, according to Von Baer, there is always found between the embryonic and the maternal part of the cotyledon a mass of thickish consistence, the origin of which is a matter of doubt. It may be derived either from the sheaths of the maternal cotyledon, or from the villi of the fœtal cotyledon, or from both. It has probably formed a layer of active organic cells, which played an important part between the two systems of vessels. When the cotyledons of the ruminants separate at the time of birth, the vascular tufts of the villi remain uninjured. The Mammalia present great varieties in the process of the separation of the placenta. E. H. Weber divides these varieties into two classes. To the first class belong those cases in which the two placentæ (the fœtal and the uterine) are so loosely connected that they separate without either receiving any injury. The uterus here suffers no lesion, and the uterine placentæ remain after birth, and merely diminish in size: this is the process in the ruminants, horses, and hogs. The second class includes those instances where the two portions of the placentæ are so intimately united that the uterine portion is torn away, together with the fœtal portion, at the time of birth. Here the uterus receives a wound, and the placentæ are deciduous organs, which must be renewed at each gestation. This class is exemplified in man, the Carnivora, and the Rodentia.*

Nutrition of the fœtus. — There is a period in the growth of the ovum which precedes the development of blood-vessels. Since the chorion and its villi are composed of nucleated cells, similar to those which are the active agents in the growth and vegetative changes of the primitive structures of the embryo, previous to the formation of vessels and the circulation of blood, the growth of the villi of the chorion long before the development of the blood-vessels is an intelligible phenomenon. These villi then attract matters from the surrounding fluids, and, like the cellular structures of plants, convey them onwards, transmitting them from one cell to another, until they accumulate in the interior of the ovum. This is the essential process in all organic absorption, even when blood-vessels and lymphatics exist; for even in the intestines the vascular villi are invested by a sheath formed of nucleated cells, which exert the same action as the cortical cells of the spongiola of the roots in plants. When the blood-vessels of the embryo have reached the chorion and its villi, these blood-vessels, which have been developed from cells and participate in the active properties of cells, absorb the nutriment. The nutritive matters thus absorbed are supplied either by the blood of the mother in which the villi float, as in the human placenta, or as in Mammalia by the white secretion of the uterine glands. The absorbed nutriment enters directly into the blood of the fœtus. The process thus maintained between the fœtal and the maternal blood supplies the process of respiration to the fœtus, or an equivalent for that process.

There is no other mode of nutrition to which great importance can be ascribed. It is true, the amnion may, by the organic action of its cells, absorb fluids from the chorion, and deposit nutriment in the form of a small quantity of albumen in the liquor amnii. The liquor amnii enters the mouth of the fœtus, and certainly reaches the intestinal canal as well as the trachea. For in the stomach of the fœtus of the human subject, as well as of mammiferous animals, there have been found hairs derived from the lanugo, or first hair of the fœtus, which falls out and becomes mixed with the liquor amnii. But this mode of nutrition by means of the liquor amnii can at most be of trifling and very inadequate amount.

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* See Froriep's Notiz. 46 Bd. p. 90. Compare Eschricht, loc. cit.

SECTION III.

Of the development of the organs and tissues in the fœtus.

CHAPTER I.

DEVELOPMENT OF THE SYSTEMS OF ORGANS, AND ORGANS.

In the preceding section the object held in view has been to give a succinct statement of the most important general phenomena of development presented by the ovum, and of their most remarkable varieties in the different classes of animals. The mention of numerous particulars, which would have obscured the general view of the subject, has been intentionally avoided. It remains now to consider in succession the development of the several systems of organs, so far as accords with the purpose of this work, and is rendered possible by the present state of our knowledge.*

The development of determinate parts from a homogeneous mass presupposes the existence of a formative substance endowed with plastic power, which contains within itself in the potential or virtual state all that is actually produced from it by development. The germ was potentially the entire animal; and the first rudimental mass of an organ bears the same relation to all the structures afterwards to be formed within it,—with this difference, that the potential germ being supplied with nutritive matter acts independently of any other power, whilst the plastic force which effects the development of the particular parts and tissues in an organ is controlled by the organic force of the whole organism, and is, as it were, delegated to the organ by this general organic force. This blastema of a part in the state of formation has, therefore, nearly the same relation to the whole system as the part when fully developed. In the lower animals the special part acts as a delegated part of the whole as long as it is connected therewith, but can be separated from the rest of the system or organic being and its controlling influence; it may then even become the foundation or germ of a new being, as we have seen exemplified in the Hydra and Planaria. (See page 1431.) Hence in those more simple animals the blastema of a part which, by the organic plastic force of the being, is caused to assume the structure and properties of a special organ, would probably, if withdrawn from that influence by separation from the rest of the being, in process of development become the stock of a new animal.

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* The works treating generally of the development of the different systems of organs, are Burdach's Physiologie, Bd. ii : Rathke's Abh. zur Bildungs-und-Entwickelungs-geschichte, Leipzig, 1832, 1833; Von Baer's Entwickelungs-geschichte der Thiere, Bd. i. und ii.; Valentin's Entwickelungs-geschichte; and Von Ammon's Chirurgische Pathologie in Abbildungen, H. i. Leipz. 1838. The principal treatises on the development of special systems and organs will be mentioned in the course of the present section.

The "blastema" must not, however, be regarded as a mere soft, plastic, gelatinous mass devoid of structure or composed only of globules, such as it appears to the naked eye or with low magnifying powers; for according to the researches of Schwann, it consists partly of a fluid, partly of granules which spontaneously change into the nuclei of cells and into cells, and partly, also, of such nucleated cells already formed. Such, be it remembered, is the substance which will be spoken of in the following pages under the designation of the "blastema" of the different organic systems; although the phenomena of the development and metamorphosis of cells in the formation of the different parts will not at present be described.

1. *Vertebral column and cranium.*

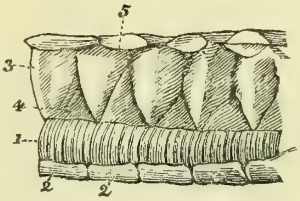
The persistent conditions of the vertebral column in many fishes, which have been described by G. Cuvier, C. A. S. Schultze, Von Baer, and myself, offer some very remarkable points of comparison with the fœtal state of the vertebræ in the higher animals.

The primitive part of the vertebral column in all the vertebrata is the gelatinous chorda dorsalis, which consists entirely of cells. This cord tapers to a point at the cranial and caudal extremities of the animal. In the progress of its development it is found to become enclosed in a membranous sheath which at length acquires a fibrous structure, composed of transverse annular fibres. (See figs. 235 and 237.) The chorda dorsalis is to be regarded as the ázygous axis of the spinal column and in particular of the future bodies of the vertebræ, although it never itself passes into the cartilaginous or the osseous state, but remains enclosed as in a case within the persistent parts of the vertebral column which are developed around it; being permanent, however, only in a few animals, whilst in the majority it disappears at an early period.

The cartilaginous or osseous vertebræ are always first developed in pairs of lateral elements at the sides of the chorda dorsalis. From these lateral elements are formed the bodies and the arches of the vertebræ. In some animals, however, the lateral elements of the vertebræ undergo no further development, and it is here that the chorda dorsalis is persistent through life.

In the myxinoid fishes the spinal column presents no vertebral segments, and there exists merely the chorda dorsalis with the fibrous layer surrounding its sheath, which is the layer in which the skeleton originates. This fibrous layer also forms superiorly the membranous covering of the vertebral canal. In the Petromyzon the same fibrous layer contains cartilaginous plates, the rudiments of the arches of the vertebræ, whilst as yet, no trace of the bodies of the vertebræ exists. In the Chimæra and Sturgeon there are cartilaginous plates upon the chorda dorsalis or its sheath both above and below,—in other words, the fibrous layer has developed superior and inferior symmetrical parts of vertebræ. (See fig. 235.) The superior lateral portions form the superior arches; the inferior form the transverse processes, and in the caudal part of the column in the sturgeon unite below so as to form inferior arches in which the extreme portion of the aorta lies. The superior and inferior parts of the vertebræ have not become united in these animals except at the most anterior part of the column, where such an union has taken place and the chorda has become wholly enclosed in cartilage.

Fig. 235.*



The vertebræ of fishes, therefore, appear to be formed by the coalescence of four symmetrical portions, the upper pair of which embrace the spinal cord, whilst the lower pair enclose the aorta in the caudal region, and in the trunk support the ribs. From the coalescence of these four rudimentary portions the bodies of the vertebræ enclosing the chorda dorsalis and its sheath at first sight appear to arise. But such is not the case; for in fishes the conversion of the sheath itself into cartilage or bone has a share in the formation of the bodies of the vertebræ. It is true that in the Sturgeon this sheath remains throughout life fibrous, but in the Chimæra it becomes ossified. In these animals the chorda remains persistent as the base of the vertebral column; but at the same time its thick sheath, on which the symmetrical cartilaginous portions of the vertebræ rest, presents thin ossified rings much more numerous than the vertebral segments. (See fig. 235.) The sheath of the chord preserves its membranous structure only internally towards the gelatine mass and on its exterior. We have evidence, therefore, in these instances, that the body of the vertebra in fishes is composed of a central and a cortical portion which have very different modes of origin. In the Sharks and Rays and the osseous fishes the same fact is equally distinct; and here the vertebræ have

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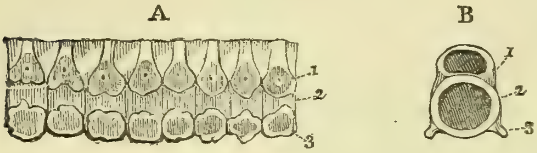
* [Fig. 235. Part of the vertebral column of Chimæra monstrosa. 1, chorda dorsalis with its sheath; 2, rudiments of the transverse processes of the vertebræ; 3, rudiments of the arches of the vertebræ, or cartilaginous crurales; 4, cartilaginous inter-crurales; 5, small cartilages completing the spinal canal above, and interposed between the pairs of arches. After Müller, Anatomie der Myxinoiden, 1834.]

undergone more or less complete ossification. In the embryos of sharks and rays the chorda dorsalis is at a certain period quite uniform in outline, whilst the superior and inferior pairs of vertebral elements in a cartilaginous state rest upon its thick sheath (fig. 236, A). Subsequently this sheath becomes constricted at intervals corresponding to the distances of the future vertebræ, begins to be divided into distinct segments, and assumes the cartilaginous or osseous state. The chorda in this way becomes constricted at successive points and divided into a series of rounded masses resting in the concave facets of the interposed vertebræ, through the centre of which they frequently communicate with each other. The layers of the vertebræ which form the facets originated in the sheaths of the chorda, and constitute the central portion of the body of the vertebra in the fish. The external layer or cortical portion is produced by the coalescence of the four primitive lateral elements (See fig. 236, B.) The mode of development of the vertebra is essentially the same in the osseous fishes. In many families, as the Cyprini and Salmonidæ, a suture can be distinguished at each side of the body of the vertebra, and in the third or fourth vertebra in Cyprini it is possible, even in the adult condition, to separate the four lateral elements or the cortical portion from the central portion of the body of the vertebra.

Fig. 236.*



In the Swordfish there is no lateral suture; but a space in which ossification has not taken place exists between the cortical and central parts of the bodies of the vertebræ. The chorda itself lies within, constricted in the situation of each vertebra, while its larger portions rest on the facets of the contiguous vertebræ.† The vertebral column is not, however, developed in all classes in the same manner.

In Amphibia and Reptiles the inferior pair of lateral elements of the vertebræ are not developed, except in the caudal region, where they form inferior arches. The development of the body of the vertebræ is effected in very different ways, in relation to the chorda dorsalis, in these classes of animals. In the frog-like Amphibia (Anoura) two principal varieties of the mode of development of this part have been observed by Dugès. In the genus Pelobates (P. cultripes seu Rana cultripes, Cuvier; Cultripes provincialis, Müller; and P. fuscus, Wagl.; Bufo fuscus, Cuvier; Cultripes minor, Müller) the chorda dorsalis is not surrounded by the bodies of the vertebræ; but the superior pair of lateral elements merely have been developed, constituting the arches, and have coalesced beneath the chorda, so as to form the body of the vertebra. The chorda, therefore, lies in a groove upon the upper surface of the bodies of the vertebræ; but it gradually wastes and disappears. The same structure exists, according to my observations, in the genus Pseudis (Rana paradoxa).

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* [Fig. 236. Part of the vertebral column of a fœtal Acanthias vulgaris. A, lateral view. 1, superior vertebral elements or arches; 2, sheath of the chorda dorsalis undergoing division into the bodies of the vertebræ; 3, inferior vertebral elements. B, the same seen in a transverse section. After Müller, Vergleichende Neurologie der Myxinoiden. Abhandl. der k. Ak. der Wissen. zu Berlin, 1838.]

† See J. Müller, Vergleichende Anatomie der Myxinoiden, Abhandl. der Akad. d. Wissensch. zu Berlin. J. 1834, and the more recent paper, Die Vergleichende Neurologie der Myxinoiden. Ibid. J. 1838, p. 232.

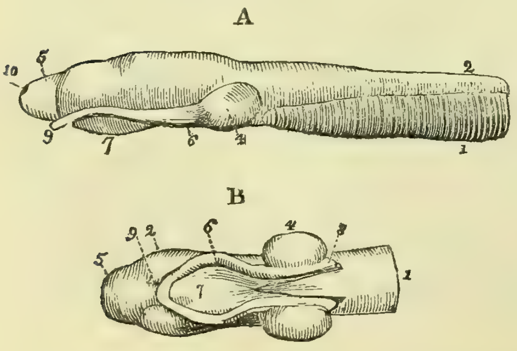
In other frog-like Amphibia, and the Salamandrinæ, the mode of origin of the body of the vertebræ is totally different. The sheath of the chorda itself becomes the seat of ossification in annular segments corresponding to the successive vertebræ, and remains membranous only in their intervals. Hence, at a certain period of the life of the larva, the chorda dorsalis is enclosed in a number of thin ossified rings, which, however, gradually grow thicker and take the place of the chorda. In this case the body of the vertebra is not formed by two symmetrical elements, and the superior pair of lateral elements of the vertebra, forming the arches, merely becomes united to the ossified rings.

In reptiles, birds, and mammals the type of formation of the vertebræ seems to be again different. The peculiarity of this type is, at all events, distinct in the class of birds. Here the vertebræ, in that part of the spinal column which belongs to the trunk, are developed from a single pair of elementary parts. When the formation of these parts from the blastema commences, there appear at each side of the chorda dorsalis a series of quadrangular figures, the rudiments of the future vertebræ. (See fig. 191, page 1538.) These gradually increase in number and size, so as to surround the chordaboth above and below, sending out at the same time superiorly processes to form the arches destined to enclose the spinal marrow. In this primitive condition the body and arches of each vertebra are formed by one piece on each side. At a certain period these two primary elements, which have become cartilaginous, unite inferiorly by a suture. The chorda is now enclosed in a case, formed by the bodies of the vertebræ, but it gradually wastes and disappears. Before the disappearance of the chorda the ossification of the bodies and arches of the vertebræ begins at distinct points.

The ossification of the body is first observed at the point where the two primitive elements of the vertebræ have united inferiorly. The form of this centre of ossification is bilobed; only in the sacral vertebræ of the bird, have I seen it in the form of two distinct ossifying points. Those vertebræ which do not bear ribs, such as the cervical vertebræ, have generally an additional centre of ossification in the transverse process, which is to be regarded as an abortive rudiment of a rib. In the fœtal bird these additional ossified portions exist in all the cervical vertebræ, and gradually become so much developed in the lower part of the cervical region as to form the upper false ribs of this class of animals. The same parts exist in Mammalia and man. Those of the last cervical vertebra are the most developed, and in children may, for a considerable period, be distinguished as a separate part on each side, like the root or head of a rib. Hence it follows, that the lower of the nine cervical vertebræ of the Sloth, which bears rudiments of ribs, are not on that account to be regarded as dorsal vertebræ, but that this animal has really nine true cervical vertebræ. The transverse processes of the lumbar vertebræ seldom present distinct points of ossification, forming false ribs; but, in the hog, at a certain period of fœtal life this is an ordinary appearance. Of the same nature are the two portions of bone which, in man and other animals, unite the sacral vertebræ on each side to the ilia. In crocodiles, tortoises, and turtles these parts of the skeleton are so elongated that the pelvis is clearly seen to be connected with the vetebral column by means of vertebral ribs.*

The true cranium is a prolongation of the vertebral column, and is developed at a much earlier period than the facial bones. Originally, it is formed of but one mass, (in which condition it remains, as the cerebral capsule, in the Cyclostomatous fishes, the Sharks and the Rays,) the chorda dorsalis being continued into its base and ending there with a tapering point. This relation of the chorda dorsalis to the basis of the cranium is persistent through life in the Cyclostomata and Sturgeon family; the acuminated extremity of the chorda reaching to about the middle of the base of the cerebral capsule. The sheath of the chorda extends to its very point. The first appearance of a solid support at the base of the cranium, which I have observed in the Ammocœtes, consists of two elongated bands of cartilage, one on the right and the other on the left side, which are connected with the cartilaginous capsule of the auditory apparatus, and united with each other in an arched manner anteriorly beneath the anterior end of the cere-

Fig. 237.†



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* See the Vergleichende Anatomie der Myxinoiden, loc. cit. p. 303.

† [Fig. 237. The rudimentary parts of the cranium in Ammocœtes branchialis; A, viewed from the side; B, seen from below. 1, internal sheath of the chorda dorsalis; 2, tube of the spinal marrow; 3, cerebral capsule; 4, auditory capsule; 5, nasal capsule; 6, palatal bands of cartilage; 7, the palatal palate or lamina, united at its borders to the palatal cartilages; 8, cartilage of the basis cranii; 9, anterior commissure of the palatal cartilages; 10, the nasal orifice. After Müller Vergleichende Anat. der Myxinoiden.]

bral capsule. (See fig. 237.) The same cartilages are present in the Myxinoid fishes, and are persistent; the facial cartilages also proceeding from them. In Ammocœtes and Myxine these basilar cartilages have the cephalic portion of the chorda dorsalis between them. In Bdellostoma the process of development has gone a step further; for here the two cartilages have wholly coalesced posteriorly and have formed a simple basilar cartilage, in which the chorda is enclosed. Hence we see that in the cranium, as in the spinal column, there are at first developed at the sides of the chorda dorsalis two symmetrical elements, which subsequently coalesce and may wholly enclose the chorda. Rathke has recently observed, in the embryos of serpents and other animals, before the formation of the proper cranial vertebræ, two symmetrical bands of cartilage, similar to those which I discovered as a persistent structure in the simplest state in Ammocœtes.*

At a later period the basis cranii of vertebrate animals contains three parts analogous to the bodies of vertebræ, the most anterior of which, in the majority of animals, is small and its development frequently abortive, whilst in man and mammiferous animals the three are very distinct. These parts are developed by the formation of three distinct points of ossification, one behind the other, in the basilar cartilage. The three ossified portions become united by sutures, and in mammals form a rod-like body tapering towards its anterior extremity and giving attachment at its sides to the lateral parts of the three vertebræ. The bodies of the three cranial vertebræ are the os basilare occipitale, the os basilare sphænoideum posterius, and the os basilare sphænoideum anterius, which in all mammals are very clearly defined. The lateral parts of the vertebræ, developed in the cerebral capsule, are: 1, the lateral parts of the occipital bone; 2, the alæ majores of the sphenoid bone; and, 3, the alæ minores of the same bone. The superior part or squama of the occipital bone, the parietal bones, and the frontal bone are developed in the cerebral capsule and complete the arches of the three vertebræ. Between the parietal bones and the occipital squama there are developed in some animals ossicula Wormiana, analogous to those bones which lie between the arches of the vertebræ in Sharks and Rays. Similar bones are developed also at the basis of the vertebral column, as in the sturgeon, and at the base of the cranium. Of this nature are apparently the ossa petrosa also, which have no exclusive connection with the auditory apparatus, and in birds and the animals below them in the scale, share with other bones the function of enclosing the labyrinth.

The squamous part of the temporal bone in man and the higher animals contributes to the formation of the true cranium, from which it is in reptiles, amphibia, and fishes more or less excluded. The proper function of this bone is to support the lower jaw. In birds, reptiles, amphibia, and fishes, several other parts, as the os quadratum and the os zygomaticum, aid in the composition of the suspensor of the lower jaw.* In young mammiferous animals two other parts can be distinguished in connection with the temporal bone, namely, the annulus tympanicus and the bulla tympani, which Hagenbach could distinguish as separate parts in some mammals. Platner saw an annulus tympanicus in several birds; and frogs also have a rudiment of the same part.

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* See Rathke, über die Entwickelung des Schädels. Königsberg, 1839.

2. *The facial portion of the skull and the "visceral arches."*

The facial region of vertebrate animals consists of the organs of sense, nose, eye, and ear, which are appended to the cranium and the cerebral vesicles contained within it, and of the upper and lower jaws and their muscles. The upper jaw, or maxillary apparatus, according to the general plan of the Vertebrata, is, in its most perfect form, composed of five bones, namely, the os intermaxillare, the vomer, the os maxillare, the os palatinum, and the os pterygoideum seu palatinum posterius. In some animals all these bones exist on each side of the face, and they may all bear teeth; but certain of them are in many animals destitute of teeth, and abortive in their development; as are, for example, in man and mammalia, the vomer, the os palatinum, and the os pterygoideum, or internal ala of the processus pterygoideus of the sphenoid bone, which, in several animals, is developed as a distinct bone, and forms a continuation of the palate backwards. In its most fully developed form the superior maxillary apparatus reaches, through the medium of the os pterygoideum, to the lower jaw; and then the upper and the lower maxillary apparatus form together a fork-like body suspended from the temporal bone. Of these parts only an imperfect palate exists in the cyclostomatous fishes, neither upper nor lower jaw being present. The organs of sense of the Vertebrata have frequently special bones provided for them, which form parts of the skeleton; such are the ethmoid bone, the nasal-bones, the supra-orbital bones of Lizards and the Python, the infra-orbital bones of fishes, and the tympanic ring. In many animals also there extends between the temporal bone and the upper jaw an arch which is completed by the malar or jugal bone.

The mode of development of the facial part of the head has of late years been investigated by Von Baer, Rathke and Reichert. Before the development of the face, the visceral cavity of the cephalic region is formed superiorly by the primitive rudimentary structure which contains the encephalon, the cerebral capsule; whilst the lower and lateral walls of that cavity are formed by the anterior " visceral arch." At this period there is no nasal cavity, and the visceral cavity of the head extends uninterruptedly from the first visceral arch to the cerebral capsule. In birds and mammiferous animals there are three visceral arches, and also three visceral clefts. The first cleft becomes converted into the external auditory passage, the tympanum and the tuba Eustachii; the second and the third are obliterated. The face is originally formed of a middle portion proceeding from the forehead, Von Baer's frontal process, and of a lateral portion on each side derived from the superior extremity of the first visceral arch. These parts are at first separate. The lateral and the inferior parts, destined to form the superior and inferior maxillary apparatus, are both, according to Reichert, derived from the first visceral arch, in which an angular bend appears; the part above this bend being converted into the superior maxillary mass, and that below it into the inferior maxillary apparatus. (See fig. 238.) The superior maxillary mass, in its growth, approaches the frontal process and unites with it; a cavity being left beneath that process and between the two superior maxillary masses, which becomes the nasal cavity. By the union of the superior maxillary masses (the superior maxilla and palate bone) of opposite sides beneath this cavity, the separation of the nose from the mouth by the palate is produced. Attached to the elongated frontal, or nasal process of the forehead, there soon appears the substance of the superior intermaxillary bone, whilst at the lower part of the visceral arch, from which the lower jaw is formed, a partly detached portion presents itself, which Reichert calls the inferior intermaxillary rudiment. It is not yet known whence the rudiment of the superior

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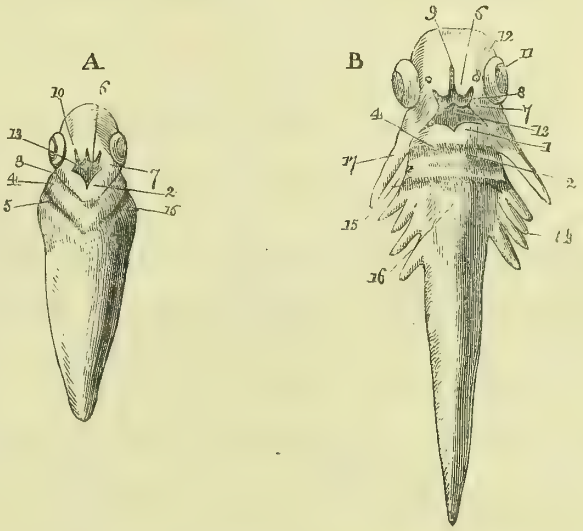
* For information respecting the comparative anatomy of these parts the reader may refer to Hallmann's valuable treatise: Vergleichende Osteologie des Schläfenbeins. Hannover, 1837.

Fig. 238*.



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* [Fig. 238. Development of the parts of the face in the embryo of Triton tæniatus. A, an embryo four lines long, magnified: B, another embryo further advanced in development. After Reichert. 1. The first visceral arch, or inferior arch of the first cephalic vertebra (incorrectly marked 2 in the figure A); 2. the second visceral arch; 3. the second visceral process; 4. the first visceral cleft; 5. the second visceral cleft; 6. the nasal or anterior frontal process; 7. rudiments of the superior maxilla; 8. rudiments of the superior intermaxillary bone; 9. the cleft between the nasal or anterior frontal processes; 10. the external nasal opening; 11. the eye; 12. the small elevation of the lachrymal bone; 13. the opening of the cephalic visceral cavity or mouth; 14. the external branchiæ; 15. the membranous branchial operculum; 16. elevated ridge pushed forwards by the heart and its aortic arches.]

intermaxillary bone is first derived; for although the blastema of this part is first observed between the nasal processes on the part of the face derived from the forehead, yet it is very possible for it to have been derived originally from the nasal processes themselves, and from the immediately contiguous, superior part of the first visceral arch. This latter view appears to me more accordant with comparative anatomy, since the superior maxillary apparatus, in its most complete form, comprehends the os intermaxillare, the vomer, the os maxillare, and the ossa palatinum et pterygoideum. There would then remain merely the middle part of the face which belongs to organs of sense, and is attached to the anterior part of the skull; and this part, in the Plagiostomatous fishes, is united with the skull, whilst the parts belonging to the upper jaw are detached from it. On the other hand, however, there are facts in comparative anatomy which favour the contrary view; for the vomer, although it arises in the middle line, yet belongs to the general category of the maxillary apparatus and dentiferous bones. In man and mammals its development is abortive, but in fishes and batrachian amphibia it contains teeth. The intermaxillary bones therefore may, very possibly, like the vomer, differ entirely from the other parts of the upper jaw in their origin. In the monstrosity called harelip, in which the upper jaw bones and palate bones of opposite sides do not meet, the right and left intermaxillary bones are united, and instead of being attached to the upper jaw bones of their respective sides, remain in the middle line; the cleft of the palate being prolonged forwards on each side between the maxillary and the intermaxillary bone, so as to leave the latter with the incisor teeth suspended to the vomer. It will be evident from the preceding description, that the palate dividing the nasal from the oral cavity does not exist during a long period of fœtal life; this septum between the two cavities not being formed until the superior maxillary masses, extending inwards from each side, meet in the middle line.

The mode of development of the face not only affords an explanation of the abnormal cleft palate and the congenital cleft between the upper maxillary and the intermaxillary bone; but also seems to throw light upon those congenital fissures which pass between the intermaxillary bone and upper jaw as far upwards as the orbital cavity. Congenital clefts of this kind, which correspond to primitive conditions of the parts, are called results of the arrest of development. But in applying this extremely fruitful theory, which Meckel's researches have rendered so important, to fissures of the integuments, some caution is necessary. The harelip, or cleft of the upper lip in the situation of the junction between the os maxillare superius and the os intermaxillare, certainly is dependent on arrest of development, but not entirely: for the upper lip is at no period of normal development cleft in this manner, but grows from its attached border uniformly at all points at the same time. The arrested development of the deeper-seated parts seems, however, to give rise to an imperfect formation of the lip.

The transformations which the visceral arches undergo in mammalia are, according to Reichert's observations, as follow: "the blastema" of the first visceral arch produces, as special structures, the superior maxillary apparatus, the under jaw, and a part of the ossicula auditûs, namely, the malleus and the incus. It was discovered by Meckel, that in the fœtus of the human subject and of mammiferous animals the malleus is prolonged at the inner side of the lower jaw-bone as far as the chin, where it forms an arch by its union with its fellow of the opposite side. There are formed, therefore, in the first visceral arch, both an inferior maxillary arch and an arch of the malleus. Reichert shows that the latter is formed first. After the development of the lower jaw, the long process of the malleus lies at the inner side of the first solid rudiment of that bone; and when the lower jaw is in greater part developed and ossified, the prolongation of the malleus begins to suffer atrophy.

From the second visceral arch are formed the suspensory apparatus of the hyoid bone and the stapes of the ear. The suspensory apparatus of the os hyoides in the human subject is at its upper part osseous, consisting of the processus stiloideus, which is at first isolated, but subsequently becomes anchylosed with the temporal bone; in its middle portion it is ligamentous, where it constitutes the ligamentum stilo-hyoideum; while most inferiorly it is again osseous, and forms the smaller cornu of the os hyoides. In most mammals nearly the whole of this suspensory apparatus becomes ossified, and constitutes the numerous segments of the anterior cornu of the os lingualis seu hyoides. The posterior cornua and the body of this bone are developed from a cartilaginous band contained in the third visceral arch.*

3. *The Extremities.*

The extremities are developed in an uniform manner in all vertebrate animals. They appear in the form of leaf-like elevations from the parietes of the trunk (see fig. 223, page 1588) at points where more or less of an arch will be produced for them within. The primitive form of the extremity is nearly the same, whether it be destined for swimming, crawling, walking, or flying. The primitive rudiment is formed according to the general type of the vertebrata, and is subsequently moulded into the specific forms. In the human fœtus the fingers are at first united by the blastema as if webbed for swimming; but this is to be regarded not so much as an approximation to the form of aquatic animals, as the primitive form of the hand, the individual parts of which subsequently become more completely isolated.*

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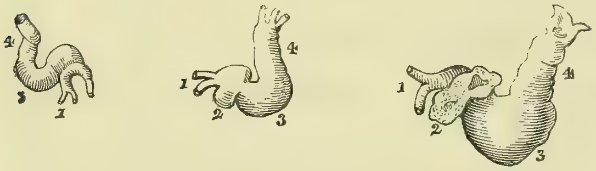
* For an account of the metamorphoses which the "visceral arches" undergo in birds, reptiles, and amphibians, Reichert's work already cited, and his Vergleichende Entwickelungs-geschichte des Kopfes der nackten Amphibien, Königsberg, 1838, may be consulted.

4. *The vascular system.*

The first development of the vascular system and heart in the germinal membrane has been already described. The earliest form of the circulation presents itself in the area vasculosa bounded by the sinus terminalis, to which the blood is distributed from the heart and aorta by means of two transverse arteries, and from which it is again returned to the heart by two veins running in opposite directions from the upper and lower parts of the area vasculosa. (See figs. 191 and 192, page 1538.) This arrangement of vessels subsequently undergoes a change; the veins above described are replaced by others which are developed from the vascular network of the area vasculosa and accompany the transverse arteries; the sinus terminalis ceases to exist, and the vessels extend over the whole surface of the yolk-sac.

The Heart.—The heart is originally in all animals a simple undivided canal, which at its lower extremity receives the venous trunks, and at its upper extremity divides into the arterial trunks or aortic arches. This canal becomes curved in a horse-shoe form, and at the same time becomes divided into three cavities (fig. 239). Of these three cavities which are developed in all vertebrata, the most posterior is the simple auricle; the middle one the simple ventricle; and the most anterior the bulbus arteriosus. These three parts of the heart contract in succession. The division of the heart into three cavities is observed in the chick about the second or third day. The auricle and the bulbus arteriosus at this period lie at the extremities of the horse-shoe. The bulging out of the middle portion inferiorly gives the first indication of the future form of the ventricle. (See fig. 239.) The great curvature of the horse-shoe by the same means becomes much more developed than the smaller curvature between the auricle and bulbus; and the two extremities, the auricle and bulb, approach each other superiorly, so as to produce a greater resemblance to the later form of the heart, whilst the ventricle becomes more and

Fig. 239.†



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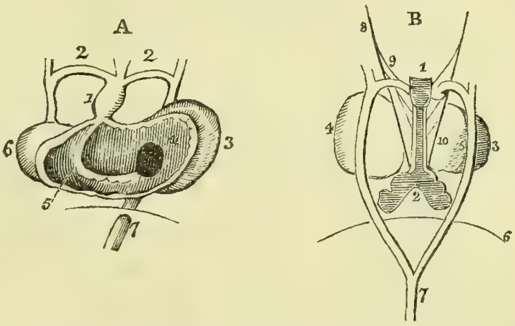
* An account of the special development of the osseous system must be sought in the more extended works on the subject of fœtal development. A complete account will be found in Valentin's "Entwickelungs-geschichte."

† [Fig. 239. Heart of the chick at the 45th, 65th, and 85th hours of incubation. 1, indicates the venous trunks: 2, the auricle; 3, the ventricle; 4, the bulbus arteriosus. After Dr. Allen Thomson, Edinb. New Phil. Journ. vol. ix. pt. ii.]

more developed inferiorly. The heart of fishes (see fig. 5, p. 160, edit. 1; p. 172, edit. 2) retains these three cavities, no further division by internal septa into right and left chambers taking place. In the amphibia also the heart throughout life consists of the three muscular divisions which are so early formed in the embryo; but the auricle is divided internally by a septum into a pulmonary and a systemic auricle (fig. 10, p. 165, edit. 1; p. 176, edit. 2). In reptiles, not merely the auricle is thus divided into two cavities, but a similar septum is more or less developed in the ventricle. In birds, mammals, and the human subject both auricle and ventricle undergo complete division by septa; whilst in these animals, as well as in reptiles, the bulbus aortæ is not permanent, but becomes lost in the ventricles. The division of the auricle and ventricle into right and left cavities begins in birds about the 60th or 70th hour. The septum dividing the ventricle, according to Von Baer, commences at the apex and extends upwards. (See fig. 240.) A communication between the two ventricles was observed by Dr. Allen Thomson still existing after 7½ days' incubation. Subsequently this opening is closed, and at the same time a septum is developed in the bulbus aortæ separating the roots of the proper aorta and the arteria pulmonalis. The septum of the auricles is developed from a semilunar fold which extends from above downwards. The left auricle, which is at first very small, is found in connection with the pulmonary veins after the sixth day. In man the septum between the ventricles, according to Meckel, begins to be formed about the fourth week, and at the end of eight weeks is complete. The septum of the auricles in man and all animals which possess it, remains imperfect throughout fœtal life. When the partition of the auricle is first commencing, the two venæ cavæ have different relations to the two cavities. The superior cava enters as in the adult into the right auricle; but the inferior cava is so placed that it appears to enter the left auricle, and the posterior part of the septum auricularum is

Fig. 240.*



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* [Fig. 240. Heart of a human embryo of about the fifth week. A, the heart opened on the abdominal aspect. 1, indicates the bulbus arteriosus; 2, two aortic arches which unite posteriorly to form the aorta; 3, the auricle (which is at this period almost quite a simple cavity); 4, the opening from the auricle into the ventricle (6), which is laid open; 5, the septum rising from the lowest part of the cavity of the ventricle; 7, the vena cava inferior. B. The same heart viewed from behind. 1, the trachea; 2, the lungs; 3, the ventricle; 4, 5, the large atrium cordis or auricle: 6, the diaphragm; 7, the aorta descendens; 8, the nervus vagus; 9, its branches; 10, continuation of the nervus vagus. After Von Baer, Siebold's Journal, Bd. xiv. and Entwickelungs-geschichte der Thiere, Bd. ii.]

formed by the great Eustachian valve, which extends from the point of entrance of the inferior cava. Subsequently, however, the septum, growing from above downwards, becomes directed more and more to the left of the vena cava inferior. During the entire period of fœtal life, there remains an opening in the septum auricularum, which the valvula foraminis ovalis, developed in the third month, imperfectly closes.*

Aortic arches and pulmonary vessels.—In the early embryos of all vertebrate animals the blood is distributed from the bulbus aortæ towards either side, and after passing round the circumference of the visceral cavity is again collected in front of the vertebral column into a single vessel, the aorta descendens. According to Serres, the aorta descendens in the chick about the 40th or 50th hour is double in its whole length. Dr. Allen Thomson observed this condition about the 36th or 40th hour; but found the two vessels already united in a considerable extent at the 48th or 50th hour. According to Reichert there is a small transverse communication even at the earliest period. The aortic arches are always several in number, and at first lie in connection with the visceral arches. In those animals which breathe by branchiæ, and in which the visceral arches partly serve for the formation of the branchial apparatus, each of the aortic arches is resolved into two parallel vessels, one arterial, which comes from the heart and ramifies wholly in the branchiæ; and the other venous, which arises in the branchial laminæ and unites with the veins of the other branchiæ in front of the aorta to form the descending aorta. In the amphibia the same structure exists for a certain period; but afterwards the branchial vessels are again transformed into three aortic arches, which, when the branchial apparatus has ceased to exist, sink deeper into the thoracic cavity and become permanent.

The Sharks and Rays and the Amphibia have either fœtal or larval branchiæ. These are distinguished from permanent branchiæ, being filaments or tufts, projecting or depending externally from the branchial cavity and containing vascular loops. The external gills of the Sharks and Rays do not exist during the whole period even of fœtal life, but disappear at a certain time, no trace of them being found in the more advanced fœtus.† The external branchiæ of some amphibia, as the Bufo obstetricans and Salamandris terrestris, are fully developed even during fœtal life, and receive blood-vessels. In frogs the external branchiæ are provided for the first few days of the larva condition, they then disappear whilst the internal branchiæ take their place. When the lungs of the frog have become developed, the pulmonary artery on each side is a branch of the most inferior aortic arch, whilst the posterior portion of this arch resembles a persistent ductus arteriosus. In the Reptilia no branchiæ or branchial vessels are developed on the visceral arches, and the several aortic arches are received into the thoracic cavity, yet continue to exist in part throughout life. The lizards have four permanent aortic arches, two on each side; whilst the tortoises, and turtles, the crocodiles, and the serpents, have only two, one of which gives off the vessels for the upper part of the body, while the other furnishes the artery for the viscera. (See fig. 6, p. 161, edit. 1; p. 173, edit. 2.) The pulmonary artery of these animals arises independently from the ventricle; but in the adult turtles and tortoises it is possible to distinguish traces of two other aortic arches which are now obliterated, but which previously had the relation of ductus arteriosi to the vessels sent from them to the lungs.

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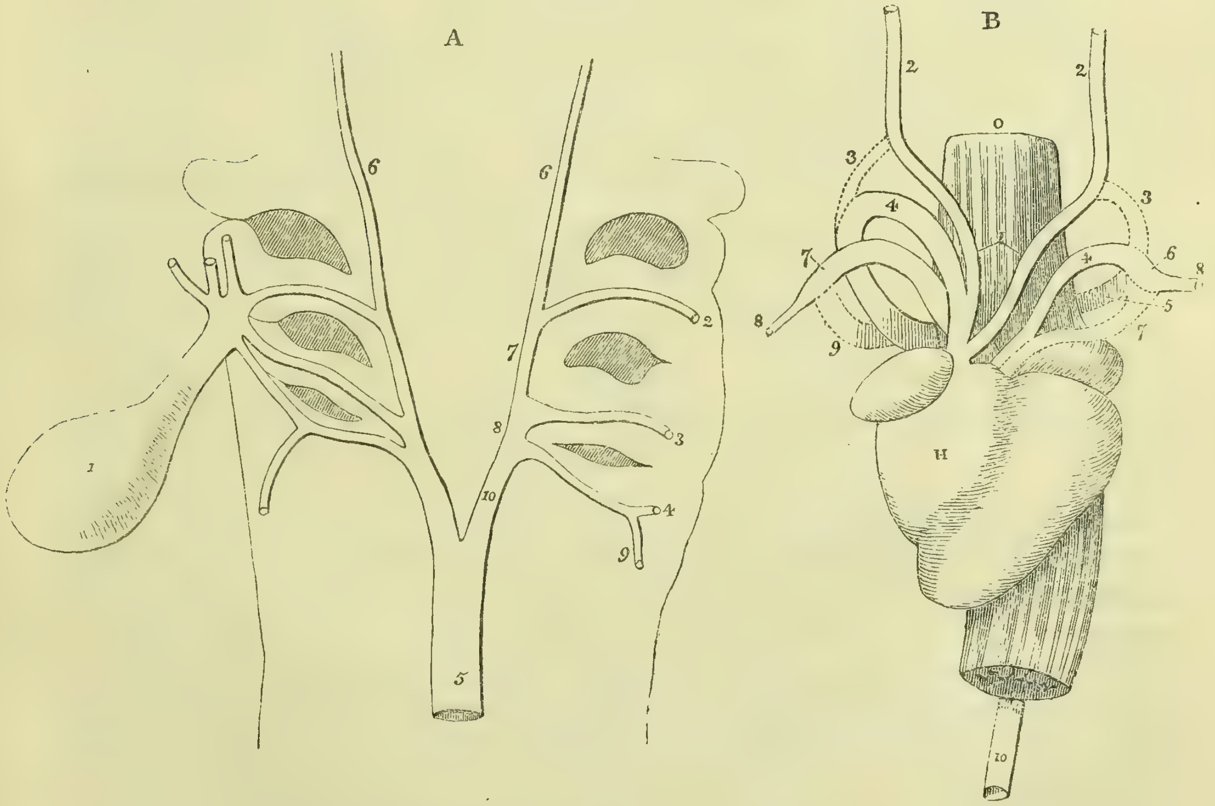
* The authors to be consulted on the development of the heart are, Meckel, Archiv. ii. p. 402; Kilian, über den Kreislauf des Blutes im Kinde, welches noch nicht geathmet hat. Karlsruhe, 1826; Allen Thomson, Edinb. New Philos. Journ. Oct. 1830; Von Baer, op. cit.; and Valentin, op. cit.

† Leuckart, über die aeusseren Kiemen der Embryonen von Rochen und Haien. Stuttgardt, 1836.

In birds there exist at a certain period of fœtal life six aortic arches. Of these the two superior furnish the arteriæ anonymæ of the upper

Fig. 241.*



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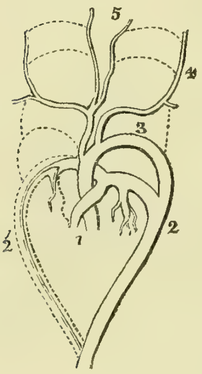
* [Fig. 241. From Huschke, Isis, 1828. A. Neck of an embryo chick at the end of the fourth day of incubation cut open in front, and the lateral halves spread out so as to show the aortic arches and the descending aorta: 1, the heart; 2, 3, and 4, the branchial arteries or aortic arches; 5, the descending aorta: 6, the arteria anonyma; 7, 8, the anastomotic branches between the first and second and between the second and third aortic arches; 9, the artery to the lungs; 10, the future ductus arteriosus. B. Plan showing the changes by which the adult condition of the great vessels arising

parts of the body. The posterior parts of this pair of arches become atrophied. The most inferior pair of arches supply the pulmonary arteries, and form two ductus arteriosi terminating in the aorta descendens, which are not obliterated until the development of the fœtus is completed. The pulmonary arteries then become independent vessels, and arise from the right ventricle of the heart by a distinct trunk, which had at an early period become separated from the aorta by a septum dividing the interior of the bulbus aortæ. Of the two middle aortic arches only the right one remains, the left being obliterated early in fœtal life.*

In Mammalia, according to Von Baer's observations, the aortic arches are soon reduced to three, one of which is the persistent arch of the aorta, whilst the other two are the ductus arteriosi of the pulmonary artery. Of these ~~ductus~~ arteriosi the right also disappears; so that during the remainder of fœtal life only two aortic arches exist, one arising from the right, and the other from the left ventricle. (Fig. 242.) The former of these gives off the arteries to the lungs, the latter the vessels to the upper parts of the body. These two arches are of equal size, and so remain until the fœtus has attained its maturity. After birth the posterior portion of the arch which arises from the right ventricle (the ductus arteriosus Botalli) rapidly becomes narrowed, and in the course of the first few weeks after birth its cavity is entirely obliterated. The anterior portion of this arch now becomes the trunk of the independent arteriæ pulmonales. At the same time the closure of the foramen ovale takes place.

Fig. 242.†



In birds the arch of the aorta is a right aortic arch—that is to say, it passes to the right of the trachea

from the heart is produced from the embryonic structure: 1, 1, the first pair of aortic arches in the embryo, giving off the arteriæ anonymæ (2, 2); 3, branches of communication between the first and second aortic arches (obliterated in the process of development); 4, 4, the second pair of aortic arches. That of the right side becomes the persistent arch of the aorta; that of the left is the future left pulmonary artery; 5, the ductus arteriosus which becomes obliterated; 6, anastomosis between the second and third aortic arch of the left side; 7, the third aortic arch: That of the left side becomes obliterated; that of the right side forms the right pulmonary artery; 8, 8, the pulmonary arteries; 9, branch of communication between the third and second arch of right side; 10, descending aorta; H, heart; O, œsophagus.]

* See the excellent papers of Huschke in the Isis, 1827, p. 401; and 1828, p. 161. Compare Allen Thomson's observations in the Edinb. New Phil. Journ. January, 1831.

† [Fig. 242. Plan of the transformation of the system of aortic arches into the permanent arterial trunks in mammiferous animals; after Von Baer. 1 indicates the situation of the original single trunk which arose from the single ventricle and which

and œsophagus in its way to the vertebral column. In man and Mammalia it is a left aortic arch passing to the left side of the parts just mentioned.

Veins.—It appears, from Rathke's excellent researches, that the conformation of the venous system also is at first the same in the embryos of all vertebrate animals, and subsequently departs in various ways from the common primitive type. In the original condition there are two anterior venous trunks (the jugular veins) and two posterior trunks, which Rathke names the cardinal veins. One of the anterior trunks, and one of the posterior unite on each side and form a transverse canal,—the ductus Cuvieri. The two ductus Cuvieri unite beneath the œsophagus to form a shorter main canal which enters the auricle,—at that time a simple cavity. The cardinal veins are originally formed by the caudal veins, branches from the kidneys and Wolffian bodies, and others from the dorsal parieties of the trunk, which are at a later period the intercostal and lumbar veins; and in animals which have lower extremities the two cardinal veins also receive the venæ crurales. This system, as it exists in all animals, may be designated the venous system of the simple auricle. It persists in most vertebrate animals as long as their heart resembles that of fishes. In fishes themselves it continues to exist throughout life. (See fig. 5, p. 160, edit. 1; p. 172, edit. 2.) In the Amphibia and Reptilia the cardinal veins become the venæ advehentes of the kidneys, which convey the blood to those organs from the hinder extremities. The common canal, formed by the union of the two ductus Cuvieri, is at a still earlier period absorbed into the cavity of the originally simple auricle in all animals above fishes; and after the septum auricularum is formed, the two ductus enter separately the right auricle. The venæ subclaviæ unite with the venæ jugulares. The ductus Cuvieri in birds and some mammals remain as two venæ cavæ superiores, or anteriores, entering the right auricle separately. In other mammals the right duct alone remains as the superior or anterior vena cava. In serpents, lizards, birds, and mammals, there is formed a distinct system of vertebral veins, the posterior of which are the vena azygos, and vena hemi-

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has become divided into two tubes. The single trunk gave off five pairs of aortic arches which terminated in the two roots of the aorta (2, 2'). Those of the arches which are obliterated at a very early period are marked by dotted lines. The first arch of the right side with the root of the aorta of that side (2') which remains longer and forms the right ductus arteriosus, is drawn as a very narrow vessel with a dotted line on each side. The vessels which still exist at birth are drawn of the full size. These are the first arch of the left side, constituting the ductus arteriosus Botalli, which is in greater part obliterated soon after birth, and the second arch of the left side, constituting the permanent arch of the aorta (3). The subclavian arteries (4) and the carotid arteries (5) are seen to be formed from parts of the other primitive aortic arches. After the obliteration of the left ductus arteriosus the pulmonary arteries are the only remains of the first pair of aortic arches.]

azygos (more correctly venæ conjugatæ, since they are perfectly symmetrical branches of a single trunk, which is a true vena azygos). The blood of the anterior and posterior vertebral veins is poured into the superior vena cava.

The omphalo-mesenteric vein, vena omphalo-meseraica, which receives the vein of the mesentery, is a primitive structure common to all vertebrate animals. It passes with the two ductus Cuvieri, originally between them, but as a separate vessel to the auricle. When the liver is formed, this vein gives branches to it, and receives from it others, the venæ hepaticæ, in birds and mammals. Between the two sets of hepatic veins the trunk of the omphalo-mesenteric vein becomes obliterated, and then the vena portæ is formed as an independent vessel conveying blood to the liver, while the same blood is carried out of the organ by the distinct venæ hepaticæ.

In fishes there is no inferior cava. In birds and mammals that vessel arises between the Wolffian bodies, and originally enters the omphalo-mesenteric vein in front of or above the liver; and hence, after the hepatic circulation is established, this vena cava receives the hepatic veins. There is no vessel in fishes analogous to this vein. In Reptilia and Amphibia the inferior vena cava receives, not only the venæ hepaticæ, but also the blood of the kidneys and organs of generation. (See fig. 12, p. 162, edit. 1; p. 180, edit. 2.) In birds and mammals the blood of most of the animal structures of the posterior part of the body enters the vena cava inferior. In rare cases of abnormal formation the vena cava fails to be developed, and then the blood from the lower parts of the body is conveyed to the superior cava, through the system of the vena azygos.*

The umbilical vein results from the union of the veins of the allantois with an anterior vein of the abdominal parietes, vena abdominalis, which is permanent in the Reptilia and Amphibia, and joins the vena portæ. The vena abdominalis anterior exists alone in the Amphibia, since they have no allantois; but in the Reptilia both vena abdominalis anterior and the veins of the allantois exist in the fœtus.

It is probable that the veins of the anterior parietes of the abdomen and the allantoic veins are at first distinct, and become united during the further development of the allantois. On this supposition, we may explain the enigmatical fact that the umbilical vein (the vein of the allantois) terminates in the vena portæ, which lies in a part of the body very distant from that at which the allantois was developed. Rathke adduces arguments in favour of this view. In man the vena umbilicalis receives branches of the epigastric vein.†

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* Stark, de Venæ azygos Naturâ. Lips. 1835.

† Burow, in Müller's Archiv. 1838, p. 44.

The umbilical vein in birds and mammals originally terminates, according to Rathke, in that part of the omphalo-mesenteric vein which is about to enter the heart, and which subsequently forms the most anterior or superior part of the vena cava inferior. At a later period the umbilical vein, like the omphalo-mesenteric vein, sends branches to the liver, while the umbilical vein and the inferior vena cava remain connected by the ductus venosus arantii.*

The circulation of the fœtus is essentially distinguished from that of the adult human subject by the mingling of the blood of the two auricles, which takes place through the opening in their septum, also by the further mixture of the blood of the two sides of the heart which is effected through the medium of the ductus arteriosus Botalli, and further by the circumstance of part only of the blood of the right ventricle being sent to the lungs. All the blood of the body, or all the blood which the two ventricles emit, except the small quantity which the lungs receive from the right ventricle is returned to the right auricle. The blood of the left ventricle is sent to the upper parts and also to the lower parts of the body ; that of the right ventricle passes chiefly through the ductus Botalli, and supplies the lower parts of the body. All this blood returns to the right auricle. Only the fractional portion which the right ventricle sends to the lungs is collected from those organs in the left ventricle. If we suppose that both ventricles emit the same quantity of blood, — since all the blood from the one and a part of that from the other return to the right auricle,—the right auricle must receive more than half the whole mass of blood,—that is, more than the right ventricle emits; whilst the left auricle must receive less than half and less than the corresponding ventricle emits. And hence it follows that a part of the blood of the right auricle must flow through the foramen ovale into the left auricle.

5. *Nervous System.*

The nervous system in its rudimentary form, consists, according to Reichert, of two laminæ meeting in a central groove, the outer borders of which gradually become elevated, and then unite so as to form a tube. In the situation of the medulla oblongata this canal seems to remain open, unless the cleft is formed again after being once closed. Between this part, the medulla oblongata, and the most anterior extremity of the canal, several vesicular enlargements, the vesicles of the brain, are developed. (See fig. 197, page 1547.) The cerebellum was observed by Von Baer immediately in front of the medulla oblongata as early as the fourth day. To produce the cerebellum the laminæ of the spinal cord, after having formed the fourth ventricle, meet again superiorly and anteriorly and enclose a short canal leading into the vesicle of the optic lobes or corpora quadrigemina, which is the largest of the cerebral vesicles. The vesicle in front of that of the optic lobes is the vesicle of the third ventricle, the first formed, and at first the most anterior of all. In front of this, however, are developed the vesicles of the cerebrum, which are at first very small. (See fig. 243, A and B.) The nerves of special sense are originally hollow processes of the ventricles, the auditory nerve arising from the fourth, the optic nerve from the third, and the olfactory nerve from the lateral ventricle. The most essential parts of the organs of sense are, therefore, in their origin, diverticula, or parts protruded from the brain. After the sixth day Von Baer could no longer detect a cavity in these nerves. After a certain period the vesicle of the corpora quadrigemina does not increase in size equally with the other parts, whilst the cerebral hemispheres become most rapidly developed, and extend so as to cover the parts situated behind them. (See fig. 243, C, D.) The great cerebral ganglia are produced by thickening of the walls of the primary vesicles ; the corpora striata in the most anterior or cerebral vesicles, and the optic thalami in the vesicle of the third ventricle. (Fig. 243, C.) On the sixth day of incubation the vesicle of the

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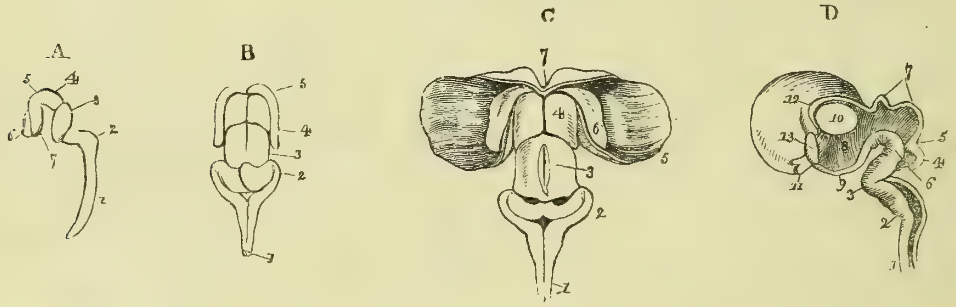
* Rathke, über den Bau und die Entwickelung des Venensystems der Wirbelthiere. Königsburg, 1838.

Fig. 243.*



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* [Fig. 243. Early forms of the brain in the embryo, after Tiedemann. A, Brain and spinal cord of an embryo of the seventh week. 1, the spinal cord ; 2, enlargement of the spinal cord where it makes a bend forwards ; 3, the cerebellum ; 4, the optic lobes ; 5, the optic thalami , 6, the membranous hemispheres of the cerebrum ; 7, prominence analogous to the corpus striatum. B, Brain of an embryo of the ninth week. 1, the spinal cord ; 2, the cerebellum ; 3, the optic lobes ; 4, the optic thalami, enclosing the third ventricle ; 5, the cerebral hemispheres. C, Brain of an embryo of the twelfth week, viewed from above, the membranous walls of the hemispheres being reflected to either side. 1, the spinal cord ; 2, the cerebellum ; 3, optic lobes ; 4, the optic thalami, between which the third ventricle lies ; 5, the walls of the hemispheres ; 6, the corpora striata ; 7, commencement of the corpus callosum. D, Perpendicular section of the same brain. 1, the spinal cord ; 2, bend of the cord forwards ; 3, second bend of the cord upwards ; 4, cerebellum ; 5, thin laminæ connecting the cerebellum with the optic lobes ; 6, crura cerebri ; 7, optic lobes or corpora quadrigemina ; 8, cavity of the third ventricle ; 9, the infundibulum ; 10, optic lobe ; 11, optic nerves ; 12, margin of the fissure leading into the lateral ventricle ; 13, the corpus callosum, at this period perpendicular in its direction.]

third ventricle was seen by Von Baer with a wide opening at its anterior part, the medullary mass having already receded from this part during the days preceding. The cerebrum, which is divided into two halves by the sinking down of its roof, being originally a part protruded from the vesicle of the third ventricle, which it overlaps, has through this cleft an indirect communication with the exterior. The great transverse fissure which subsequently leads between the optic thalamus and the fornix into the interior of the cerebrum probably is produced from the same cleft of the third ventricle by the division extending laterally, in such a manner as to leave the fornix forming the margin of the fissure, as it does in the adult. Von Baer regards as the primitive rudiment of the fornix, the boundary between the cavity of the vesicle of the third ventricle and the two cavities of the lateral ventricles; and if the cleft of the third ventricle already existing be supposed to be extended towards either side through the boundary here indicated, the great transverse fissure of the cerebrum will be produced. The borders of this fissure will then be on one side the thickened walls of the vesicle of the third ventricle (the optic thalamus), and on the other the border of the vesicle of the lateral ventricle, namely, the posterior pillar of the fornix. The glandula pinealis is, according to Von Baer, the elevated and subsequently shrunken roof of the third ventricle. The origin of the corpus callosum of Mammalia, only a trace of which is met with in other animals, is not yet known with certainty. Von Baer regards the anterior pillars of the fornix as identical with the original central depression of the cerebrum, and supposes that the walls of the hemispheres again apply themselves to each other and unite superiorly, since otherwise the ventricle of the septum lucidum could not be formed. The spinal marrow of the fœtus differs from that of the adult in containing a trace of the primitive canal, and in reaching much lower in the cavity of the spinal column.*

Among the permanent forms of the brain in the animal kingdom those of the Petromyzon and Ammocœtes are remarkable for their resemblance to the form of the fœtal brain in the higher animals, Amphibia, reptiles, birds, and mammals. The brain of these fishes possesses a special vesicle of the third ventricle, with an opening in its roof, and also a vesicle of the corpora quadrigemina. Both of these primitive parts are, in the osseous fishes, united into one large vesicle, which consequently cannot be compared to any single division of the brain of the higher vertebrata.†

The nerves are probably developed simultaneously in their whole length, from the centre to the organs for which they are destined. The reality of either a centrifugal or a centripetal development of the nerves can by no means be demonstrated.

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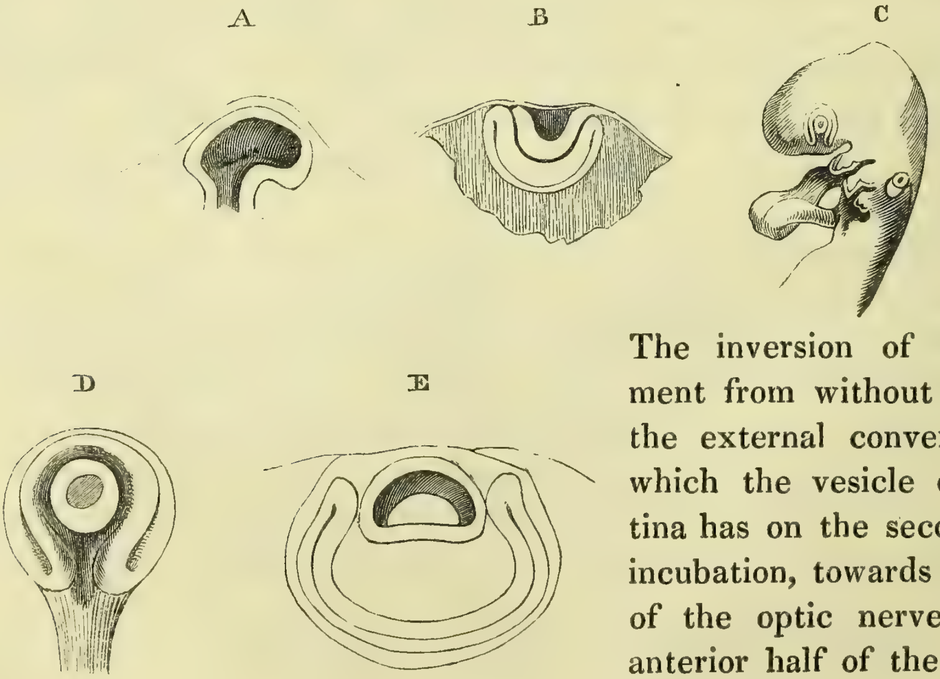
* Von Baer, Entwickelungs-geschichte I. und II. Compare Meckel, Archiv. 1815. Tiedemann, Anatomie und Bildungs-geschichte des Gehirns, Nürnberg, 1816.

† J. Müller, Vergleichende Neurologie der Myxinoiden.

6. *Organs of Sense.*

The eye is in part developed as a protruded portion of the vesicle of the third ventricle of the brain, and it contains part of the membranes of the brain, namely, the fibrous and the vascular tunic. At a certain period of development there is observed at the inner side of the eye in all animals a fissure, which was regarded by Von Baer as an attenuated part of the retina, but which has been demonstrated by Huschke to be a real fissure. In the eye of fishes the retina presents throughout life, a cleft running from the centre towards the anterior border. The retina is originally a vesicle-like protrusion of the brain, with the cavity of which it communicates through the medium of the tubular optic nerve (fig. 244, A). According to Huschke's more recent researches the cavity of the optic vesicle in the fœtal chick begins to diminish from the second day of incubation, and subsequently is reduced to the space which exists between Jacob's membrane and the retina (fig. 244, B). The sac of the transparent media which the eye afterwards contains at no period communicates with the cavity of the brain. The capsule of the lens appears, from Huschke's observations, to be developed from an inverted portion of the common integuments, and consequently is at a certain period open externally (fig. 244, B).

Fig. 244.*



The inversion of the tegument from without depresses the external convex surface, which the vesicle of the retina has on the second day of incubation, towards the canal of the optic nerve, and the anterior half of the vesicle is thus reflected inwards upon itself in the manner of a serous sac. The inverted layer becomes the future retina; the external layer, the membrana Jacobi. The true cleft in the bird's eye, according to Huschke's present view, is not formed until the third day,—not before the lens is developed; and he regards it as a consequence of the inversion of the retina. The depression produced by the pressure of the capsule of the lens upon the primitive optic vesicle is nearly round, but becomes elongated towards the canal of the optic nerve and towards the middle line of the body. This part of the depression becomes converted into a furrow (fig. 244, C. D). The apparent cleft is merely the appearance produced by this furrow or depressed fold, its margins consisting on each side of two laminæ. Consequently, it does not lead into the cavity of the tubular optic nerve.*

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* [Fig. 244. Development of the eye ; after Huschke. A. Longitudinal section of an eye of an embryo chick of two days, enlarged thirty times. The cavities of the

The iris appears to be at first wanting at the anterior border of the membrana choroidea, unless this border of the choroid itself should be regarded as the rudiment of the iris. In the human embryo the margin of the choroid at its inner and lower side, which afterwards becomes the lower side, is originally notched or fissured; but the circle of the iris is complete at its first development. The coloboma iridis or cleft of the iris at its lower part is so far a malformation resulting from arrest of development, as its origin is connected with the existence of this primitive fissure of the choroid. But the connection of the fissure of the iris with the original arrest of development appears to be similar to that which subsists between the fissure in hare-lip and the imperfect development of the more deeply seated structures; for the coloboma seems to arise from the imperfect development of the iris in the situation of the fissure in the choroid.†

retina and optic nerve are seen, the whole being covered by the external tegument C, the cephalic part of an embryo chick of the first half of the third day of incubation, magnified seven times; showing the eye with the capsule of the lens still open, surrounded by the retina, which is folded so as to consist of two layers, and presents the cleft inferiorly. There are also seen the tubular looped heart, three branchial or visceral arches, and the labyrinth of the ear still open. B, is a section of the eye of the same embryo, through the middle of the lens, enlarged thirty times. The semicircular layers of membrane are seen. The most internal is the very thick capsule of the lens; the next is the true retina, the most external is the external layer of the retina or Jacob's membrane. D, is the eye of a chick of the third day of incubation, showing the same parts as figure C on a larger scale. E, is the section of an eye at the fourth day of incubation of the chick, magnified thirty times. The capsule of the lens is now closed, is covered with conjunctiva, and contains a conical nucleus, the lens. The vitreous humour is developed between the capsule of the lens and the retina, external to the two layers of the retina is the sclerotic coat.]

* Von Baer, op. cit.; Huschke in Ammon's Zeitschrift für Ophthalmologie, 1835, p. 272.

† Compare Seiler, über die Ursprünglichen Bildungs-fehler des Auges Dresden, 1833.

The eye of the fœtus of Mammalia and Man is characterised by the possession of a delicate membrane closing the pupil, the membrana pupillaris, the blood-vessels of which are derived from the anterior surface of the iris. The latter circumstance and the attachment of the membrane not exactly at the margin of the iris, but somewhat in front of the margin and rather to its anterior surface, render it probable that this membrana pupillaris is continued over the anterior surface of the iris, and perhaps lines the whole anterior chamber of the eye. From the pupillar margin of the iris there likewise extends backwards the vascular membrana capsulo-pupillaris, which connects the margin of the capsule of the lens with the margin of the iris. The blood-vessels of this membrane are derived from the capsular branch of the arteria centralis retinæ, which penetrates the vitreous body, and reaching the posterior wall of the capsule of the lens gives off a number of twigs which radiate towards its circumference. These radiating vessels, however, do not belong to the lenticular capsule itself, but are prolonged into the vessels of the membrana capsulo-pupillaris, which at the margin of the pupil anastomose with the vessels of the pupillary membrane and iris. By maceration the membrana capsulo-pupillaris can sometimes be separated from the proper pupillary membrane, which in these cases appears to have a distinct posterior lamella belonging to the structure of the former membrane. This lamella with the capsulo-pupillary membrane and the vascular membrane investing the anterior concavity of the vitreous body, forms a shut sac, to the posterior wall of which the capsule of the lens is applied, while between the anterior part of the sac, which is united with the pupillary membrane and the capsule of the lens, the posterior chamber of the eye lies. Both the vessels of the pupillary membrane and those of the capsulo-pupillary membrane communicate with the vessels of the iris.*

The eyelids of the human subject and mammiferous animals, like those of birds, are first developed in the form of a ring. They then extend over the globe of the eye until they meet and become firmly agglutinated to each other. But before birth, or in the Carnivora after birth, they again separate.

The ear likewise consists of a part developed from within and of one formed externally. The labyrinth is developed upon the hollow protruded part of the brain which forms the auditory nerve. It appears first in the form of an elongated vesicle at the hinder part of the head of very young embryos above the second so-named branchial cleft. In the Cyclostomatous fishes this primitive form of the labyrinth is retained, at least by its hard parts. According to the researches of Valentin the labyrinth of the fœtus appears first as a separate body of a roundish but somewhat elongated form. The inner end of the cavity of this body soon becomes more elongated, and while it begins to make a circular turn forms a second roundish vesicle which is the rudiment of the cochlea. The convolutions of the cochlea are then formed in the following manner. The wall of the primary vesicle of the cochlea becomes, as it were, excavated from the interior, first in the direction from the vestibule towards the basis of the cranium, and afterwards in a spiral course, till it reaches the point which becomes the summit of the perpendicular axis or modiolus. In this way are produced the external form resembling that of a turbinated shell, and internally a deep furrow or half-canal, the walls of which in their windings approach each other more and more closely by their inner borders, and at length coalesce, so that they surround a cylindrical or rather a conical body, the axis of the convolutions. The conversion of the groove of the cochlea into a complete tube takes place in different animals at different periods of development. The semicircular canals of the internal ear of Mammals are produced, according to the same observer, as diverticula of the vestibule, which terminate by again communicating with the same cavity.*

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* Henle, de membranâ pupillari, Bonnæ, 1832. Reich, de membranâ pupillari, Berol, 1833. Valentin, Entwickelungs-geschichte. B. Langenbeck, de Retinâ. Gott. 1836. Krause, in Müller's Archiv. 1837, p. xxxv.

The Eustachian tuba, the cavity of the tympanum and the external auditory passage, according to the observations of Huschke,† are remains of the first so-named branchial cleft. The membrana tympani divides the cavity of this cleft into an internal space the tympanum, and an external meatus. The systems of tegumentary structures, the mucous membrane of the mouth, which is prolonged in the form of a diverticulum through the Eustachian tube into the tympanum, and the external cutaneous system come into relation with each other at this point, the two membranes being separated only by the proper membrane of the tympanum. The origin of the ossicula auditûs has already been mentioned (page 1619). Their ossification commences in the human subject as early as the fourth month.

The development of the nose is described at page 1617.

7. *Alimentary or digestive canal.*

The alimentary canal is at first an uniform straight tube, which gradually becomes divided into its special parts, stomach, small intestine, and large intestine. The stomach originally has the same direction as the rest of the canal; its cardiac extremity being superior, its pylorus inferior. The first changes of position which the alimentary canal undergoes, consist in the stomach assuming an oblique direction, and in the small intestine taking a new course from the stomach towards the navel, and, after making an abrupt bend there, returning towards the middle of the body in order to make its final curve to reach the anus. The limit between the small and the large intestine lies in the part returning from the umbilicus, the ductus omphalo-entericus being connected with the lower part of the small intestine. (See plate iv. fig. 4.) At this point of the intestine the canal frequently presents a diverticulum in the adult, and the existence of this abnormal structure has a relation to the original communication subsisting between the intestine and the duct of the umbilical vesicle. The part of the small intestine near the umbilicus gradually becomes elongated and convoluted (see plate iii), and at the same time the large intestine rises so as to form its great arch around the greater part of the small intestine.* The mode of development of the peritoneum and mesentery has been described at page 1530.

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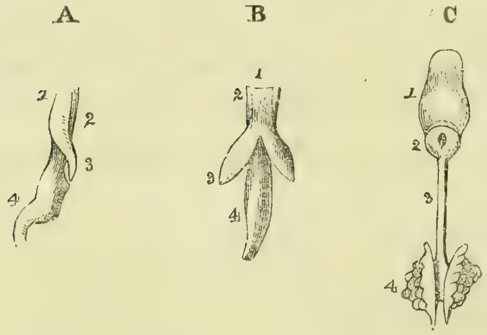
* Valentin, Entwickelungs-geschichte, p. 206.

† Isis, 1831, p. 951.

The mesentery has at first, like the intestinal canal, a straight direction, and the stomach has then its mesogastrium extending from its greater curvature to the middle line of the posterior wall of the abdominal cavity. The process by which this mesogastrium together with the stomach itself acquires a transverse position, is converted into the great omentum, and subsequently becomes connected with the transverse colon, has already been detailed. (See p. 497, edit. 1 ; and p. 544, edit. 2.) It has also been shown that the spleen is originally developed within the mesogastrium, and consequently is, no less than the mesenteric glands, a symmetrical organ.†

8. *Respiratory apparatus.*

Fig. 245.‡



The lungs, whose origin has already been pointed out (at p. 1556), appear as small tubercles on the abdominal surface of the œsophagus. They are united at the anterior part of their circumference, and here a pedicle is formed which becomes elongated into the trachea. (See fig. 245, A, B.) Soon afterwards the lung is seen to consist of a mass of cæcal tubes issuing from the branches of the trachea. (Fig. 245, c.)*

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* See Meckel's Archiv. 1817. Müller ibid. 1830.

† The development of the liver, pancreas, and salivary glands is described at pages 446 to 452, edit. 1, and pages 488 to 494, edit. 2.

‡ [Fig. 245 illustrates the development of the respiratory organs. A. is the œsophagus of a chick on the fourth day of incubation, with the rudiments of the trachea and the lung of the left side, viewed laterally. 1, the inferior wall of œsophagus ; 2, the upper wall of the same tube ; 3, the rudimentary lung ; 4, the stomach. B, is the same object seen from below, so that both lungs are visible. C, shows the tongue and respiratory organs of the embryo of a horse. 1, the tongue ; 2, the larynx ; 3, the trachea ; 4, the lungs viewed from the upper side. After Rathke.]

With respect to the diaphragm, it has been observed by Von Baer that the earlier the period of development at which it is examined the nearer is its position to the anterior part of the body. For example, in fœtal pigs half an inch in length, in which the heart lay but just within the trunk, he found the superior border of the diaphragm attached at the most anterior part of the trunk, apparently to the first dorsal vertebra. Von Baer was able to recognise the diaphragm distinctly when the yet undivided ventricle of the heart was scarcely received into the cavity of the trunk.

9. *The Wolffian bodies, urinary apparatus, and sexual organs.*

The Wolffian bodies were first discovered by C. Fr. Wolff, but were regarded by him as rudiments of the kidneys. Oken recognised their existence in Mammalia. Meckel also observed them in the human subject; but was not aware of their true nature and compared them to the epididymis. Rathke afterwards examined them in birds, mammals, and reptiles, and ascertained that the kidneys were independent of them, but still believed that they became the epididymis in the male, while in the female they disappeared. They appeared to be absent in fishes and amphibia, while they were found in all animals which had an allantois and an amnion, and hence their existence seemed to be in some way connected with the presence of these membranes. It is quite true that they are absent in fishes; but I have detected them both in the fœtus and in the larva of batrachian amphibia. Here they have a distinct excretory duct and a position so far removed from the organs of generation as well as from the kidneys, (namely, in the most anterior part of the abdominal cavity close beneath the branchiæ,) that they seem to be quite independent of both of those systems of organs, and in mammals I have found the epididymis likewise independent of the Wolffian body, lying between it and the testicle in connection with which it is developed. The Wolffian bodies are without doubt secreting organs, since they have excretory ducts which open into the cloaca; and in the fœtal bird I have seen within their secreting tubes and their excretory duct a whitish yellow matter which could be pressed from one part of the tubes to another. The observations of Jacobson, also, that uric acid can be detected in the fluid of the allantois of the bird's egg at a very early period of incubation, whilst the kidneys are not visible before the sixth day, renders it probable that the Wolffian bodies have the same function as those organs,—that they are primary or temporary kidneys bearing the same

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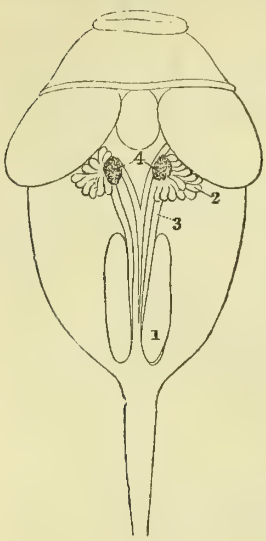
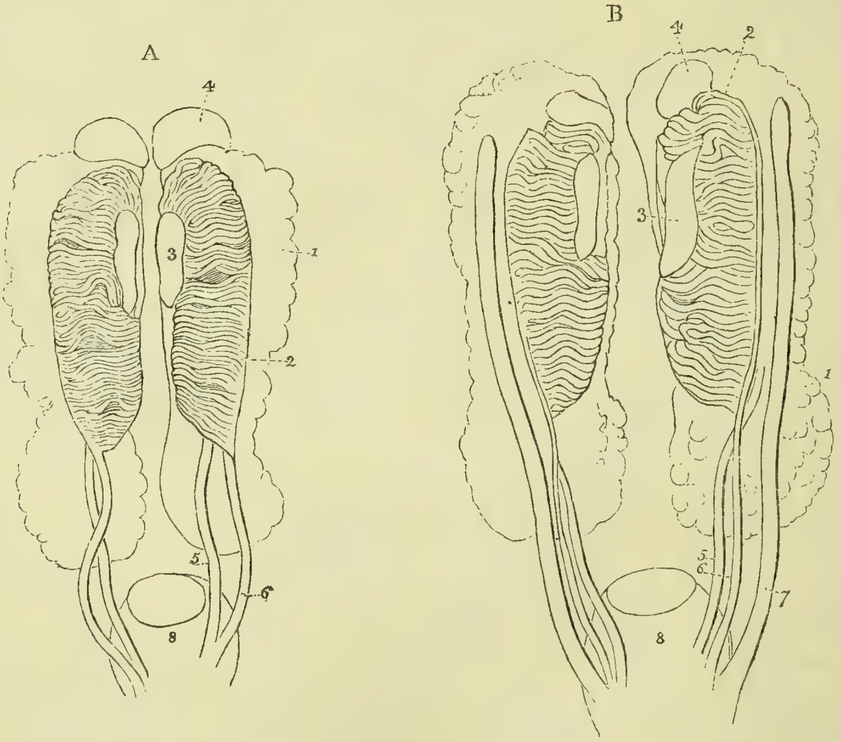
* The process of the development of the trachea and larynx is minutely described by Von Baer, op. cit.; Rathke, Nov. Act. t. xiv. pt. i. p. 162; and Valentin, op. cit. p. 49.

Fig. 246*



relation to the persistent kidneys as the branchiæ of Amphibia do to the lungs which succeed them. The presence of the Malpighian corpuscules of the kidneys in the corpora Wolffiana, as observed by Rathke, is favourable to the same view. The duration of the existence of the Wolffian bodies is very different in the different classes of Vertebrata. It is longest in the Amphibia. In the larvæ of the frogs and Salamanders each of these organs consists of a bunch of cæca situated at the most anterior part of the abdominal cavity, from which an excretory duct passes backwards along the side of the vertebral column. (See fig. 246.) Here they exist during the whole period of the larva state. In birds the Wolffian bodies are developed on the third day of incubation. They extend from the heart to the posterior extremity of the body of the embryo, and consist of cæcal tubes united by one excretory duct which opens on each side into the cloaca. (See fig. 247.) Behind the Wolffian bodies are formed the kidneys, and above these the

Fig. 247.†



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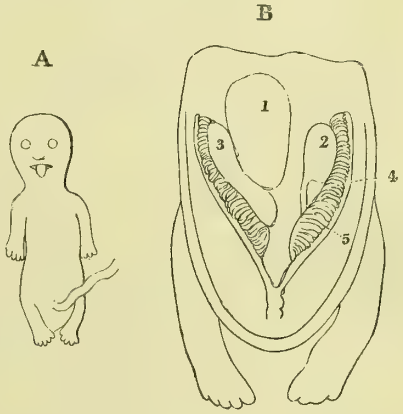
* [Fig. 246. Larva of a frog. View of the posterior part of the cavity of the trunk. 1, the kidneys; 2, the Wolffian bodies; 3, its excretory duct; 4. . . . . . After Müller.]

† [Fig. 247, shows the Wolffian bodies, kidneys, and organs of generation in a male (A), and in a female embryo of a chick (B). The parts indicated by cyphers are the following:—1, the kidneys; 2, the Wolffian bodies; 3, the testis in the male and the ovary in the female; 4, the supra-renal capsules; 5, the ureters; 6, the ducts of the Wolffian bodies; 7, the Fallopian tube; 8, the cloaca. After Müller.]

suprarenal capsules. While the kidneys increase in size, the Wolffian bodies gradually grow smaller. The testicles or ovaries are developed in front of them, and in the female or hen-bird there is always seen an oviduct* distinct from the duct of the Wolffian body. (See fig. 247, B.) In the male I have been able to detect no vas deferens distinct from the excretory duct of the corpus Wolffianum; but on the contrary the testicle and the excretory duct of the former body seemed to become connected by means of vasa efferentia. (See fig. 247, A.) As development advances the Wolffian bodies diminish in size, and after the chick is hatched merely the remains are found lying upon the kidneys.

In mammalia the Wolffian bodies are bean-shaped, and are composed of transverse cæca. (See fig. 248, B, 4.) The kidneys (2) and suprarenal capsules (1) are developed behind them. Their size is at first so great, that they entirely conceal the kidneys; but in proportion as the latter bodies increase in size, they grow relatively smaller, and come to be placed more inferiorly. Their excretory duct leads from the lower extremity of the organ to the sinus urogenitalis of the fœtus. Along the outer border of the gland runs the efferent part of the generative apparatus (5), viz. the Fallopian tuba or the vas deferens, which at first have the same conformation, and terminate by a free extremity; whilst the testicle or ovary (3) is formed independently at the internal excavated border of the organ. Subsequently the efferent tube and the testicle in the male become connected by transverse vessels, whilst in the female the extremity of the efferent tube merely acquires an open mouth. In both sexes the Wolffian bodies entirely disappear, and are not converted into any other organ. The epidydimis is developed independently, that part which consists of the coni vasculosi being formed of the communicating tubes which connect the efferent tube with the testis, and the rest being constituted by the convolutions of the efferent tube itself. All that part of the efferent tube of the generative apparatus which is thrown

Fig. 248.†



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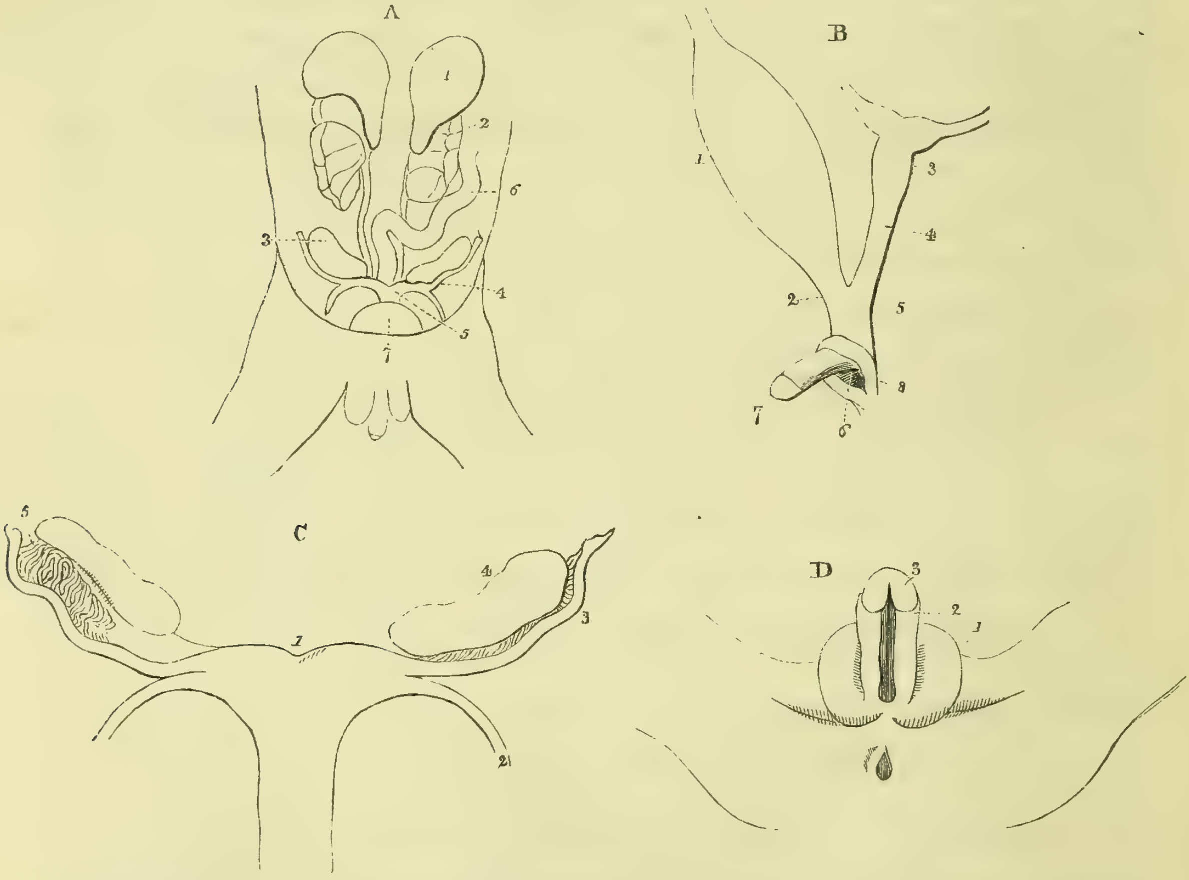
* The right ovary and oviduct become atrophied in most birds with the exception of the predaceous birds.

† [Fig. 248.—A. Human embryo measuring eight lines in length. B. Magnified representation of the urinary and generative organs of the same embryo: 1. the suprarenal capsule of the right side, totally concealing the corresponding kidney which lies behind it; 2. the kidney and ureter of the left side exposed by the removal of the suprarenal capsule; 3. the testis or ovary of the right side; 4. the Wolffian body; 5. the Fallopian tuba or vas deferens. After Müller.]

into strongly marked convolutions along the outer border of the Corpus Wolffianum contributes to the formation of the epidydimis, and from the point where the convolutions cease, a band or ligament, the gubernaculum testis Hunteri, which was developed before those convolutions of the tube were visible, passes off to the inguinal canal. In the female the tube remains free from convolutions, but from the same point as in the male a ligament, afterwards the ligamentum uteri teres, extends to the inguinal ring. The part of the tube which lies below the point of attachment of this ligament becomes the cornu uteri. In those animals in which a middle portion or body of the uterus exists, this part is formed by the coalescence of the two cornua. In the human uterus the two cornua gradually become shorter and shorter, and are lost in the body or fundus of the uterus which is at the same time developed. (See fig. 249, A, C.) In the human subject the Wolffian bodies can be detected only

Fig. 249.*



* [Fig. 249. Urinary and generative organs of a human embryo measuring 3½ inches in length. A. General view of these parts: 1. suprarenal capsules; 2. kidneys; 3. ovary; 4. Fallopian tuba; 5. uterus; 6. intestine; 7. the bladder. B. Bladder and generative organs of the same embryo viewed from the side: 1. the urinary bladder; 2. urethra; 3. uterus (with two cornua); 4. vagina; 5. part as yet common to the vagina and urethra; 6. common orifice of the urinary and generative organs; 7. the clitoris. C. Internal generative organs of the same embryo: 1. the uterus; 2. the round ligaments; 3. the Fallopian tubes; 4. the ovaries; 5. the remains of the Wolffian bodies, D. External generative organs of the same embryo: 1. the labia majora; 2. the nymphæ; 3. the clitoris. After Müller.]

in the earliest period of development, their disappearance taking place here much sooner than in quadrupeds. Traces of these organs, however, can be discovered by means of the microscope in the fold of the peritoneum which connects the ovary and Fallopian tuba as late as the middle of utero-gestation, or even later. (See fig. 249, c.) It might be supposed that in ruminants and hogs the Wolffian bodies and their secreting tubuli are converted into the Malpighian canals observed by Malpighi and Gartner, lying at the sides of the uterus and opening into the vagina; but it is by no means proved that such is the case.

The ovarium of mammiferous animals, according to the observations of Valentin,* is originally composed of tubes in which the Graafian follicles are developed.

A sinus urogenitalis has been referred to as existing in the embryos of mammals and man. This is a cavity or canal, opening externally, in which the excretory ducts of the Wolffian bodies, the ureters, and the efferent parts of the generative apparatus terminate internally. This canal is also prolonged into the urachus. Subsequently it becomes divided by a process of division extending from before backwards, or from above downwards, into a "pars urinaria" and a "pars genitalis." The former, extending towards the urachus, is converted into the urinary bladder, whilst from the latter are formed the vesiculæ seminales in the male and the middle portion of the uterus in the female. (See fig. 249, B.) The external parts of generation are at first the same in both sexes. Tiedemann perceived about the fifth or sixth week the opening of a cloaca where he had observed no opening previously. At the tenth or eleventh week the anal aperture and the orifice of the sinus urogenitalis become separated by a transverse band. The opening of the genito-urinary apparatus has the same characters in both sexes. Soon it is seen to be bounded by two folds of skin, whilst in front of it there is formed a penis-like body surmounted by a glans, and cleft or furrowed along its under surface. The borders of the furrow diverge posteriorly, running at the sides of the genito-urinary orifice internally to the cutaneous folds just mentioned. (See fig. 249, B, D.) In the female this body becoming retracted forms the clitoris, and the margins of the furrow on its under surface are converted into the nymphæ, or labia minora, the labia majora pudendæ being constituted by the great cutaneous folds. In the male fœtus the margins of the furrow at the under surface of the penis unite (about the fourteenth week), and form that part of the urethra which is included in the penis. The large cutaneous folds at a later period, namely, in the eighth month of development, receive the testicles, which descend into them from the abdominal cavity. Sometimes the urethra is not closed, and the deformity called hypospadia then results. The appearance of hermaphroditism may in these cases be increased by the testes being retained within the abdomen. This condition is merely the result of an arrest of development of the male sexual organs, and may be attended with all the feelings of the male sex and other signs of virility. There are indeed hypospadiacs in whom the defect of development is so great that even in other respects the character of the male sex is not fully maintained. But these imperfect male individuals are still by no means true hermaphrodites. Hermaphroditism consists in the coincidence of male and female organs in the same individual—for example, in the presence of all the male sexual organs together with a uterus and Fallopian tubes, though without an ovary. It is not certain that a case of perfect hermaphroditism, with both the male and the female productive organs, (the testis and ovary,) has ever yet been observed in the human species. Amongst insects hermaphrodites, with male organs on one side and female organs on the other, are not rare.

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* Müller's Archiv. 1838, p. 530.

As long as the testes remain in the abdominal cavity they are held fixed by a covering of peritoneum, the reflected parts of which form for each a suspensory band or mesorchium. They at this time have no tunica vaginalis. In their descent through the inguinal canal they follow the "gubernaculum testis;" but in front of them there passes through the inguinal canal into the scrotum, though independently of their descent, a purse-shaped prolongation of the peritoneum, the processus vaginalis peritonei. The testis, together with its mesorchial fold of peritoneum, sinks into this bag or purse-like prolongation of that membrane, and since the neck of the bag closes above the testis generally before birth, this organ lies in a distinct serous cavity, the tunica vaginalis testis, which does not communicate with the abdomen. Sometimes this neck of the tunica vaginalis remains open after birth, and gives rise to the hernia inguinalis congènita.

In the kidneys of the fœtus the pyramidal bodies are separate from each other, each covered with a layer of the cortical substance; but subsequently they coalesce. The suprarenal capsules are not proportionally of large size in the fœtus of mammiferous animals; but in the human fœtus they are of very great relative size, so as at first even entirely to conceal the kidneys.* [The most recent observations on the development of the organs in the fœtus, will be found detailed in the Appendix.]

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* Concerning the development of the Wolffian bodies, the generative and the urinary organs, consult J. Ch. Müller, De genitalium evolutione; Halæ, 1815. Rathke, Beiträge zur Geschichte der Thierwelt 3, and Abhandl. zur Bildungs- und-Entwickelungs-geschichte. J. Müller in Meckel's Archiv. 1829, and Bildungs-geschichte der Genitalien, Düsseldorf, 1830. Jacobson, Ueber die Primordialnieren, Copenhagen, 1838. Valentin, Entwickelungs-geschichte; Tiedemann, Anatomie der kopflosen Missgeburten, Landshut, 1813, p. 84; Seiler, De testiculorum descensu, Lips. 1817.

CHAPTER II.

Development of the animal tissues.

In several parts of this work mention has already been made of the recent observations respecting the organic cells, their development, and the phenomena which they present. A connected account of these observations must now be given. Modern vegetable Physiologists had already arrived at the result that the different tissues of plants, such as cellular tissue, woody fibre, ducts and spiral vessels are all originally developed from cells. The mode of formation of these cells has been explained by Schleiden.* He has shown that they are produced from the "nuclei" of Robert Brown, and hence he calls these bodies "cytoblasts" [*κύτος* a cell, *βλαστὸς* a germen]. The cytoblast is generally of a yellowish colour, and internally of a granular structure. In its interior Schleiden has detected a second nucleus (nucleolus) called by him the nucleus corpuscule, which sometimes resembles a mere spot, at other times a hollow globule. The cytoblasts are developed in a mass of mucous granules contained within previously existing cells. As soon as they have attained their full size, a delicate transparent vesicle rises upon the surface of each. This is the young cell, which at first bears the same relation to the flat nucleus as the watch-glass bears to a watch. When the cell has increased in size the cytoblast appears merely as a solid body included in the wall of the cell. The layer which now covers the cytoblast on the side towards the interior of the cell is extremely delicate,—indeed, seldom to be recognised by the eye,—and it soon becomes wholly absorbed, while the cytoblast itself disappears at the same time. The newly developed cells lie free in the cavity of the parent cell, and, as they grow and exert reciprocal pressure against each other, assume the polyhedral form.

The following are the more important observations of Schwann† respecting the cells of animals and the agreement of animals and plants in their ultimate structure.

In the chorda dorsalis, the cellular structure of which I had myself long since pointed out, Schwann first discovered the nuclei or cytoblasts. Each cell of the chorda dorsalis of Pelobates fuscus has its disk-like cytoblast lying at the inner surface of the wall of the cell; and in this nucleus there is seen one, rarely two or three, clearly defined spots. In the cavity of the cells young cells are developed, as in plants.

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* Müller's Archiv. 1838, p. 137.

† Froriep's Notizen, 1838, No. 91, 102, 112. Schwann, Mikroscopische Untersuchungen über die Ueber-einstimmung in der Structur und dem Wachsthum der Thiere und Pflanzen, Berlin, 1838. [A review of this work with a copious abstract of its contents is contained in the 9th volume of the British and Foreign Medical Review.]

Cartilages also are, according to Schwann's observations, composed entirely of cells, when first formed. The cartilaginous branchial rays of fishes at their apex are composed of small polyhedral cells, lying in close contact with each other, and having very thin walls. These cells have rounded granular nuclei. Towards the middle of the branchial ray the septa between the cavities of the different cells formed by their walls, gradually become thicker. Nearer to the root or base of the branchial ray the walls of the contiguous cells can no longer be distinguished from each other, and the mass appears to be formed of a homogeneous substance containing small cavities; but around some of the cavities a circular line can be distinguished which indicates the boundary of the wall of the cell, and proves that the whole mass is not formed by the thickened walls of the cells, but that a real intercellular substance also exists. Even while the walls of the cells are still in contact with each other, this intercellular substance is present, appearing here and there like a triangular space between three contiguous cells. (See fig. 250.) In this form of cartilage the process of development consists partly in the thickening of the walls of the cells and partly in the production of an intercellular substance. In higher vertebrate animals the thickening of the walls of the cells is not observed, and the principal mass of the future cartilage appears to be formed by the intercellular substance in which the cells with the younger cells within them are included. The development of cells in the manner of the cells of plants has been observed

Fig. 250.*

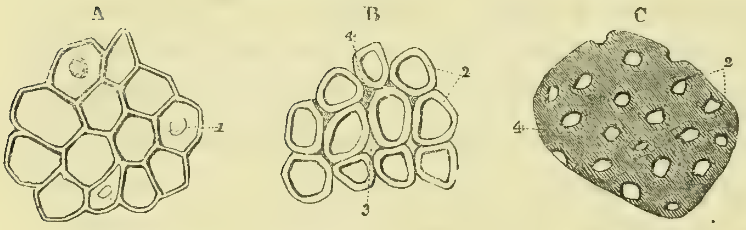
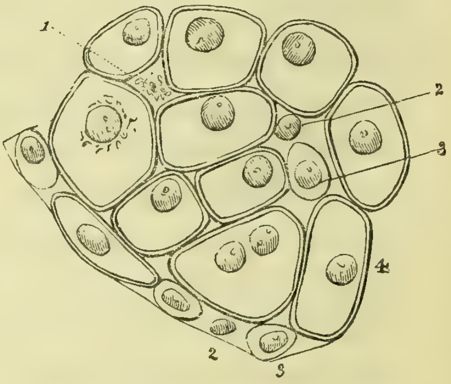


Fig. 251.†



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* [Cartilage of the branchial ray of Cyprinus erythrophthalmus. A, from the extremity of the ray; B, from the middle of the ray; and C, from its root. 1, Nucleus of a cell. 2, walls of the cells. 3 and 4, intercellular substance. In one cell two nuclei are seen. Magnified about 450 times.]

† [Cartilage from the extremity of a branchial cartilage from a tadpole. The lower margin of the figure represents the natural margin of the cartilage. Magnified about 450 times.]

by Schwann in the branchial cartilages of Pelobates fuscus, in which some cells contain mere nuclei; others, nuclei with small cells developed upon them and scarcely larger than themselves; others, again larger fully formed cells. So that here all the stages of the development of a cell are present. (See fig. 251.) The process of the development of cartilage seems to be independent of blood-vessels and to be wholly analogous to the process of growth in vegetable tissues. How the canals radiating from the corpuscules of ossified bone are developed is not known. Two hypotheses are proposed by Schwann. If the osseous corpuscules are the cavities of cells the thickened walls of which have coalesced with each other and with the intercellular substance so as to form the mass of the cartilage of the bone, then the radiating canaliculi must be regarded as canals extending from the cavities of the cells through their thickened walls, and would be analogous to the pore-like canals of some vegetable cells. But if the osseous corpuscules are the cells themselves and not merely their cavities, the whole substance between the corpuscules being intercellular substance; in this case the canaliculi will probably be radiating prolongations of the cells extending into the intercellular substance. According to the latter view, which Schwann regards as the more probable, the canaliculi would correspond to the processes given off from some cells of plants.

Besides the formation of young cells in the cavities of previously existing cells, Schwann has observed their development in the exterior of other cells in a structureless substance, the cytoblastema. In this case also the nucleus generally appears to be first formed and the cell to be afterwards developed around it. In many animal tissues the new cells are formed on the exterior of the earlier cells. In the one case the cytoblastema exists in the interior of the cells already existing; in the other it is external to them.

Schwann arranges the tissues of the animal organism, according to the mode of their development, in five classes:

I. Isolated independent cells which either float free in a fluid, or if deposited in contact with each other are still unconnected and movable.

II. Independent cells arranged so as to form a continuous membrane.

III. Tissues formed of cells, the walls of which have coalesced, while their cavities remain distinct.

IV. Fibre-cells,—cells which have become elongated in different directions and resolved into bundles of fibres.

V. Cells, both the walls and the cavities of which have coalesced, so as to form tubes.

To the *first class* belong the corpuscules of the blood. The vesicular nature of these bodies was observed by C. H. Schultz. Their nucleus, as Schwann remarks, remains attached to the inner surface of their membranous parietes when they are rendered turgid by the action of water. The red colouring matter of the corpuscules is to be regarded as the contents of the cells. The lymph corpuscules, the globules of mucus and those of pus belong to the same class. They are all nucleated cells.

To the *second class* belong the horny tissues, the pigment membranes, and the tissue of the crystalline lens.

1. *Epithelium.*—Generally composed of round cells, to the inner surface of whose parietes a nucleus containing one or two nucleoli is attached. When united into a membrane they are polyhedral. In the epithelium of the skin of a frog Schwann saw two nuclei in one cell, and also a nucleated epithelium cell within another larger cell, a fact which Henle has not observed in Mammalia. The epithelium cells, at first globular, undergo modifications of form in one or two directions. Either they acquire the form of perpendicular cylinders, as in the epithelium of the intestinal mucous membrane, described by Henle; or they become flattened into laminæ, which have the nucleus in the middle of one surface and which sometimes are elongated or riband-shaped, as in the epithelium of blood-vessels according to Henle. In the latter case it is observed that the young cells are found beneath the older ones, and are at first globular, but become more and more flattened as they approach the free surface of the epithelium.

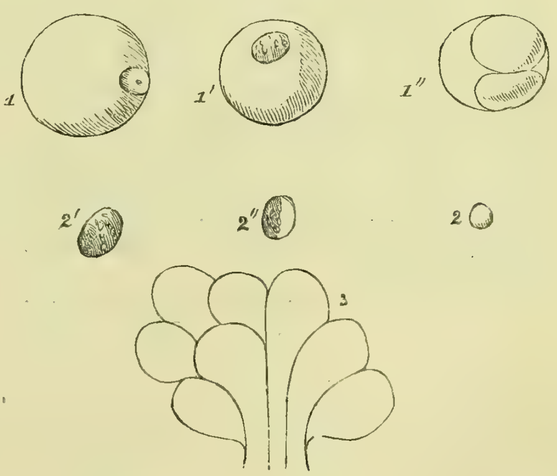
2. *Pigment cells.*—These have a nucleus at one part of their parietes, which produces the well known white spot in the middle of some pigment cells. The nucleus has usually one or two nucleoli. Many pigment cells in the process of their growth send out hollow fibre-like processes in different directions, so as to become stellate cells.

3. *Nails.*—The nail of a fully developed human fœtus consists of laminæ lying horizontally one upon the other. These laminæ become less and less distinct at the inferior surface of the nail, in proportion as the part examined is nearer to the root of the nail which is inserted into the fold of the skin of the finger; and the posterior half of this portion of the nail presents nothing of a laminated structure, but consists merely of polyhedral cells with distinct nuclei. Laminæ of the nail treated with acetic acid separate into scales in which an indistinct nucleus can in very rare cases be observed. The polyhedral cells of the root of the nail must become flattened into these scales, and the nail ought consequently to become thinner towards its free margin. This is probably prevented by the formation of laminæ of epithelium at the under surface of the nail. The horny tissue of the hoofs of animals also consists in the fœtus entirely of cells.

4. *Feathers.* — The medullary substance of feathers is composed of polyhedral cells. In the young feather a nucleus is visible in the wall of each of these cells. The cells are developed around small nuclei which lie in great number in a finely granular matter. This formation of new cells takes place not in old parent cells but near the surface of the vascular matrix of the feather, which affords the cytoblastema. Some of the nuclei contain nucleoli. The fibres of the cortical part of the shaft of the feather are produced from large band-like epithelium cells which contain nuclei and nucleoli. These cells become resolved into several fibres while all trace of the cell disappears. The barbs of the feather are themselves miniature feathers; the secondary shafts have the same structure as the main shaft, while the secondary barbs or barbules in their turn consist at first of nucleated cells applied to each other by their edges.

5. *The crystalline lens.*—The fibres of the crystalline lens are developed from the cells first observed by Werneck. In the lens of a chick after eight days' incubation there are as yet no fibres, but merely pale round cells, some of which contain a nucleus. In lenses further developed some of the larger cells contain one or two smaller cells in their interior. In embryo pigs, measuring 3½ inches in length, the greater part of the fibres of the lens is already perfect; but a part is still not completely formed; and there are besides many round cells which are about to undergo their metamorphosis. The perfect fibres compose a nucleus-like mass in the centre of the lens. The next fibres are seen to be tubular prolongations of globular cells. (See fig. 252.) The dentated borders of these cells, like those of some vegetable cells, are formed subsequently.

Fig. 252.*



Class III.

1. *Cartilages.*—Their structure and mode of development has already been described.

2. *The teeth.* — The enamel of a tooth not yet fully formed retains the same form and structure after it has been treated with dilute acid. The inner surface of the enamel membrane which envelops the crown of the tooth is formed of short hexagonal fibres, placed perpendi-

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* [Fig. 252. Cells of the crystalline lens of a fœtal pig; 1 and 1′ cells with nuclei; 1″, a cell with two young cells enclosed; 2, nuclei; 2′, an isolated nucleus with two nucleoli; 2″, a nucleus with a young cell developing upon it; 3, cells elongating themselves into fibres. After Schwann.]

cularly, so that each fibre of the enamel membrane corresponds to a fibre of the enamel. These fibres of the enamel membrane appear to be elongated cells. In the fresh state they contain a nucleus with nucleoli. Beneath these prismatic fibres of the enamel membrane is a layer of round cells which probably represent the primary condition of those fibres. The true enamel fibres probably separate from the enamel membrane, coalesce with the enamel already formed, and at the same time become impregnated with calcareous salts. The substantia propria, or ivory, of the tooth is formed of fibres, between which the dental tubuli run. The pulp of the tooth at its surface consists of cylindrical cells which contain nuclei with nucleoli. The interior of the pulp is composed of round nucleated cells. Schwann conjectures that the fibres at the surface of the pulp are in successive layers added to and converted into the growing dental substance.*

Class IV.

1. *Cellular tissue.*—In the development of cellular tissue there first appears a structureless cytoblastema, in which round nucleated cells are subsequently formed. These cells become transformed into spindle-shaped bodies, which have in their interior, but attached to their wall, a round or oval nucleus, while this nucleus in its turn includes one or two dark points (nucleoli). These elongated cells become more and more drawn out at their extremities, and give off fibres, which are sometimes branched; and at length become resolved at each end into a fasciculus of extremely delicate fibrils. The division of the fibre-like prolongations of the cells into more minute fibrils gradually extends towards the centre of the cell, so that at a later period the fasciculus of fibrils proceeds immediately from the body of the cell. Lastly, the division into fibrils takes place even in the situation of the nucleus of the cell, and then the cell becomes wholly resolved into a fasciculus of fibres, upon which the nucleus lies. (See fig. 253.) The fibres are probably tubular.

The cells of adipose tissue which are found even in the cellular tissue

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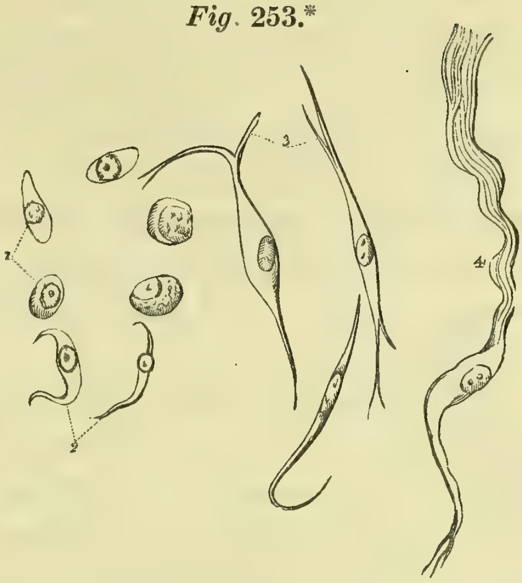
* In the first volume of this work the author described the growth of the teeth as taking place by a process of apposition in successive layers, and merely remarked that in the genera Myliobatis and Rhinoptera amongst the Plagiostomatous fishes there was an exception to the general rule, since in these instances, according to my observations, the plate-like teeth attained their full size before the calcareous salts were deposited in them. Schwann supposes that in the higher animals the fibre-like cells on the surface of the pulp are in succession converted into the ivory of the tooth, the pulp being as it were converted into cartilage and then ossified. If this be the case, the processes of chondrosis and ossification must advance by successive strata. The researches of Mr. Owen (Ann. des Sc. Nat. 1839, Oct. Odontography, pt. i.) [and those of Mr. Nasmyth (Three Memoirs on the Development and Structure of the Teeth and Epithelium. London, 1841)] confirm this view.

Fig. 253.*



of the fœtus present at first a distinct nucleus attached to their membranous wall. When the wall of the cell is thin, the nucleus forms a prominence above the surface of the fat globule contained in the cell. When the wall of the cell is thick, the nucleus is entirely included in its thickness. The nucleus contains one or two nucleoli. The fat cells in the cranium of a young fish (Plötze) sometimes have each two nuclei which bear the same relation to the membranous wall of the cell. In the cellular tissue of the fœtus a third kind of cells is met with. These are round and pale; each has a nucleus with one or two nucleoli attached to their wall; they do not become elongated into fibres, contain no fat, but are filled with granules; and this deposit of granules is first formed about the nucleus.

The cellular tissue of the fœtus, when submitted to boiling, yields no gelatine; but in its place a substance which resembles pyine, except in the particular that the turbidity produced in the solution by hydrochloric acid is removed by the addition of an excess of the acid.

2. *Tendinous tissue.*—The fibres of tendinous tissue are formed from cells, in the same way as those of cellular tissue.

3. *Elastic tissue.*—The middle coat of the arteries in embryo pigs, six inches in length, contains numerous isolated cells, some of which are globular, and some have an oblong form, while others give out two or more branching processes of various length. At the inner surface of the wall of each of these cells lies the usual nucleus with one or two nucleoli. In addition to the cells thus variously modified, fully developed elastic tissue is also present. The branching fibres of elastic tissue, which, according to Purkinje, are hollow tubes, appear to be formed from the cells just described.

Class V.

In the development of the tissues of this class there are first formed independent cells, which either are round or cylindrical, or have a stellate form. In the former case the primary cells arrange themselves in longitudinal series, their walls coalesce at the points of contact, and the septa thus formed between the cavities of the different cells are subsequently absorbed, so that in place of several primary cells one secondary cell is produced. This secondary cell now continues to grow as the simple cells grow. In this way the fibres of muscles and nerves appear to be developed. In the case of the stellate primary cells the radiating processes of contiguous cells unite, and their walls becoming absorbed at the points of union, a network of communicating canals is formed. This seems to be the process by which capillaries are developed.

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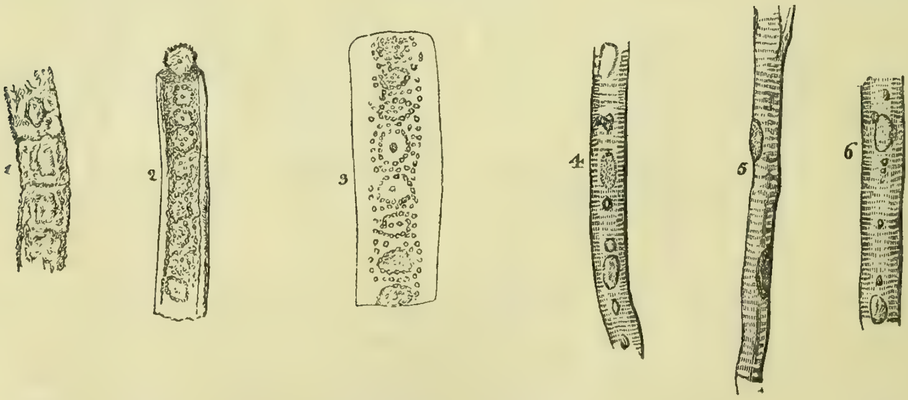
* [Primary cells in different stages of development into fibres of cellular tissue taken from beneath the cutaneous muscle of the neck of a fœtal pig, which measured seven inches in length. After Schwann. Magnifying power about 450 times.]

1. *Muscles.*—Valentin had observed that the primitive fasciculi (fibres) of muscles are formed by granules arranging themselves in a linear manner and coalescing; but that the primitive fibres (fibrils) are produced by the subsequent division of the primitive bundle. Schwann has remarked that the primitive fasciculi in the muscles of a fœtal pig, measuring 3½ inches in length, present a dark border—and a middle, more transparent part, probably a cavity. In this more transparent part he perceived besides some small granules a series of larger oval flat bodies, which appeared to be the nuclei of cells, and frequently contained one or two smaller corpuscules,—their nucleoli. These nuclei lay at pretty regular distances from each, in the thickness of the cylinder, but external to its axis. In muscles more advanced in development, the primitive fasciculi present no indication of a cavity; but the nuclei remain visible for a long period, frequently producing slight prominences on the surface of the cylinders. (See fig. 254.) According to recent observations of Rosenthal the nuclei are still present in the muscular fibre of adult animals. The proper substance of the muscular fibres is produced by a deposit taking place within the tube. (The

Fig. 254.*



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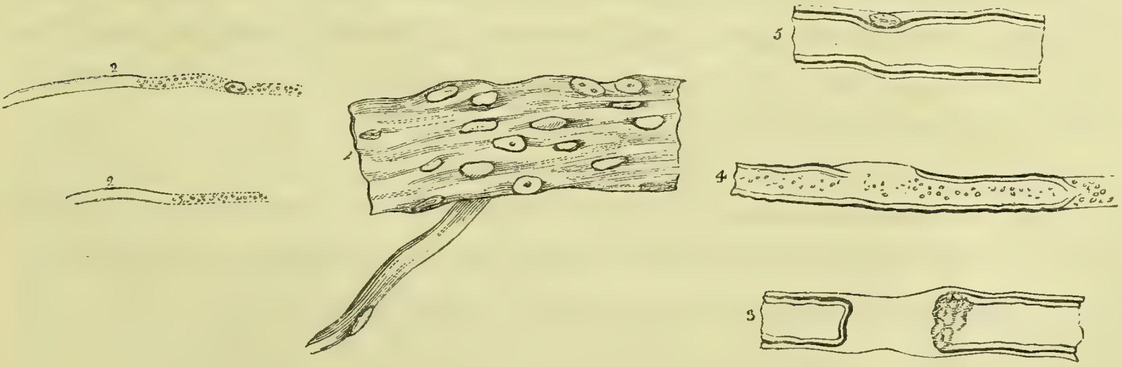
* [Development of muscular fibre after Schwann. 1, 2, 3, are fibres from the dorsal muscles of a fœtal pig, 3½ inches in length. 3, represents the fibre (2) after the action of acetic acid. 4, 5, 6, are fibres from the muscles about the humerus of a fœtal pig, which measured 5 inches in length. 5, shows the fact of the nuclei being attached to the wall of the tube; in 4 and 6, is also seen the gradual deposition of the substance from which the fibrillæ are formed on the inner surface of the tubular fibre. Magnifying power about 450 times.]

structureless sheath of the primitive muscular fasciculus, which I observed long since in insects, appears to be the remains of the tube formed by the united walls of the primitive cells.)

[According to the late observations of Valentin* there are first visible in the blastema of muscle nuclei with nucleoli, which soon become surrounded by extremely delicate cells. These cells assume an oblong figure and arrange themselves in linear forms like filaments of confervæ. On the inner surface of the membranous walls of the tubes or secondary cells formed by the coalescence of the primary cells, longitudinal striæ or fibres are deposited, while the septa dividing the tube into compartments are absorbed. The muscular fasciculus then has the form of a tube, with proportionally thick walls which are composed of perfectly transparent longitudinal fibrils. The nuclei of the primary cells are contained in the cavity of the tube.]

2. *Nerves.*—Each entire nervous fibre is to be regarded as a secondary cell, formed by the coalescence of a series of primary nucleated cells. Schwann is of opinion that the white substance of the nervous fibre, which forms a tube around Remak's band-like axis of the fibre, or the cylindrical axis of Purkinje, is a secondary deposit on the inner surface of the membranous wall of the secondary cell. He finds that the white substance of each nervous fibre is invested externally by a peculiar structureless sheath like that of the primitive muscular fasciculi. This membranous sheath can be distinguished as a transparent border external to the opaque white substance of the fibre. (See fig. 255.) Its defined outline is opposed, Schwann remarks, to the view of its being composed of cellular tissue. In perfectly formed nervous fibres Schwann some-

Fig. 255.†



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* Müller's Archiv. 1840, p. 197.

† [Development of the nervous fibres after Schwann. 1. Portion of nerve from a fœtal pig four inches in length. 2. Nervous fibres from a fœtal pig six and a half inches in length. 3 and 4. Fibres from the nervous vagus of a calf, in which the nervous matter has been displaced at one point while the transparent tube remains. 5. Nervous fibre from the same nerve, displaying a nucleus apparently contained in the membranous tube of the nerve. Magnifying power about 450 times.]

times perceived here and there at the side of the fibre a nucleus which lay included in the transparent border formed by the membranous sheath. In the grey nervous fibres no white substance is formed.

[In the substance of the brain of young embryos Valentin observed cells on the outer surface of which a granular mass was gradually deposited. These cells subsequently became nuclei; and their former nuclei became nucleoli; while the granular matter deposited around them formed the mass of the ganglionic globules which were thus developed. Valentin has also observed that after the development of nervous fibres, nuclei, elongated fibre-cells, and fully developed fibres of cellular tissue are formed around them.*]

Schwann's discoveries are to be ranked amongst the most important steps by which the science of physiology has ever been advanced. They afford the basis for a general theory of vegetation and organization which it had hitherto been impossible to frame. Valuable observations had been made in all parts of physiology, and some branches of the science had been brought to a high state of perfection. But as regards the fundamental principles on which all should rest, these it must be confessed were either very unstable or entirely wanting, and hence the slight connection which seemed to subsist between different important observations in parts of the science which were far advanced. These fundamental principles are now attained. Schwann himself has pointed out with equal lucidity and acuteness the general conclusions which are to be deduced from the observations of Schleiden and himself, and has framed from them a theory of the organization and vegetation of organized beings. It is not possible to give in this work more than the principal features of his theory.

There is one common mode of development observed in the formation of the most different elementary tissues of plants and animals, and that is the development from cells. In a pre-existing structureless substance, which may be situated either within or on the exterior of cells already formed, new cells are developed in a manner regulated by determinate laws, and these new cells undergo various modifications and transformations by which they are converted into the elementary organic tissues. In every tissue the new cells are formed only in those parts to which new nutritive matter has direct access. On this alone depends the difference subsisting between the vascular and non-vascular tissues. In the former, the nutritive fluid, the liquor sanguinis, is distributed through every part of the tissues, and hence new cells are formed through its substance. In the non-vascular tissues, on the contrary, the nutritive fluid has access to one surface only, as in the case of the epidermis. Hence in cartilages, also, when they are destitute of vessels, the new cells are formed only at their surface, or to a slight depth, namely, as far as the liquor sanguinis, their cytoblastema, penetrates. The expression, growth by apposition, is correct, when understood to signify the development of new cells, and not the growth of those already existing; for in the epidermis new cells are formed only at the inferior surface of the membrane, whilst in the vascular tissues the new cells are developed in the whole substance of the tissue. In both cases, however, the cells themselves grow by intus-susception. Cartilage is at first destitute of vessels, and the new cells consequently are formed only in the vicinity of the external surface. But after vessels have extended into the medullary canals, the formation of new cytoblastema and new cells can proceed not only on the surface of the bone but also around each of these canals. This explains the structure of the cartilage of bone, the lamellæ of which are concentric, partly around the whole bone, and partly around the medullary canals. The process by which the primary cells are formed is the following. The cytoblastema, which is at first structureless or only finely granular, presents after a time round corpuscules. These corpuscules are in their earliest recognisable condition the nuclei of cells, around which cells are subsequently to be developed. The nucleus is granular, and may be either solid or hollow. The part of the nucleus first formed is the nucleolus. Around this there is deposited a layer of fine granules. The nucleus thus formed increases in size, and then the cell is developed around it by the deposition of a layer of substance different from that of the surrounding cytoblastema. This layer has at first no defined outline; but when it has become consolidated into a membrane, it expands by the continued addition of new molecules in the interstices of the old ones. It thus becomes removed from the surface of the nucleus, which remains attached to one point of the wall of the cell. This formation of the cell around the nucleus is only a repetition on a larger scale of the process by which the nucleus was formed around the nucleolus. The membranous wall of the cell differs in its chemical properties in different kinds of cells, and even in the same cells it varies in chemical composition at different periods of its growth. Thus the walls of vegetable cells, when first formed, are, according to Schleiden, soluble in water, which is not the case with the cells which are perfectly developed. The matter contained in the cells varies in a still greater degree; for example, it is in one case fat, in another pigment. In a cell which is at first perfectly transparent a granular deposit may gradually appear, its formation commencing around the nucleus; or, on the other hand, a granular deposit contained in a cell may be gradually dissolved. [More recent information on the subject of this chapter will be found in the Appendix.]

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* Compare Valentin's observations on the development of tissues in Wagner's Physiologie, p. 132. [Willis's translation, p. 214.] Henle's observations on the Structure of the tissues in his Symbolæ ad Anatomiam cet. Berol, 1837. Müller's Archiv. 1838, p. 102. Froriep's Not. n. 294.

SECTION III.

Of birth and the changes of development which take place after birth.

CHAPTER I.

OF BIRTH.

a. The process of birth.

In nine solar or ten lunar months the development of the human embryo is completed. During this period the uterus serves as the medium of communication between the maternal system and the fœtus, and itself undergoes an increase of substance, by the constant development of new muscular fibres [of organic life]. These muscular fibres are developed by the same process as that by which muscles are originally formed in the embryo; hence at this period all the stages in the development of this tissue may be observed simultaneously in the uterus.* The muscular power of the uterus, however, remains in a latent state. When the process of development is complete, the child becomes independent of the maternal system, and is as it were a foreign body in the uterus, which reacts against it by muscular contractions. These contractions of the uterus are the cause of birth. Similar contractions of the uterus, however, occur even when the fœtus is not contained in its cavity, (in graviditas extra-uterina,) at the time of the interruption of the physiological connexion between the mother and the child. The contractions of the uterus being attended with the violent compression of living structures, are generally productive of pain, and hence are called "pains." They recur at regular periods, but even in the intervals of the "pains" the uterus is not relaxed but continues to embrace its contents. After birth the contractions of the uterus are still repeated for a certain length of time, and are then called "after-pains." In women who have died before giving birth to their child, contractions of the uterus have frequently taken place after death, and have caused the expulsion of the fœtus when the mother has been no longer living. The uterine contractions appear to commence at the os uteri, to be propagated towards the fundus, and again to return thence towards the mouth of the uterus. By this succession of muscular contractions the fœtus is first raised and then propelled downwards towards the os uteri, when the lips or sphincter of the latter part become thinned and dilated. These movements, like those for the expulsion of the urine or fæces, when energetic, are aided by the muscles of the abdominal parietes and the diaphragm, which diminish the capacity of the abdominal cavity from above, from the front, and from the sides. The action of these voluntary muscles under these circumstances is involuntary and regulated by the law of the consentaneous movements as well as by that of the reflected movements; for the uterus is the seat both of violent movements and of intense impressions on sensitive [or centripetal] nerves. At the same time many of the muscles of the trunk exhibit a tendency to consentaneous effort; the extremities seek points of resistance; the breath is held; and the arms seize anything which is capable of giving support during the contraction of the abdominal cavity. In the last month of pregnancy the uterus sinks lower in the pelvis. Towards the termination of the period of utero-gestation, also, the position of the fœtus is such that its long axis corresponds to the long axis of the uterus, and that some part, generally the head, applies itself to the os uteri or "presents" itself. The knees of the child are drawn up, the arms folded across the breast, and the head pressed down towards the sternum. In the process of birth the parts of the child, passing through the pelvis, adapt their longest diameter to the longest diameter of each region of that cavity, and hence they make a spiral turn. In the most frequent cases, those in which the head presents, the process is generally as follows. The antero-posterior diameter of the inlet of the pelvis will not allow the passage either of the greatest (antero-posterior) diameter of the head or of the breadth of the hips of the child, but the head of the child can pass with its long diameter either in the transverse or in the diagonal or oblique diameter of the pelvis. Birth begins by the long diameter of the head of the child being placed in the oblique diameter of the inlet of the pelvis. As the successive pains cause the head to descend lower, its long diameter comes to correspond with the antero-posterior diameter of the cavity of the pelvis, so that in the most common variety of head presentations the vertex and occiput are now placed under the pubes, while the face looks towards the hollow of the sacrum. In consequence of the curvature of the canal of the pelvis, the part of the child which descends along the anterior wall of the cavity travels through a very small space, while the part descending along the posterior wall describes a large arc of a circle.

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* [Not less remarkable is the development which the nerves of the uterus undergo during pregnancy. These nerves have been dissected with great labour both in the impregnated and in the unimpregnated uterus by Dr. R. Lee, and are described by him in the volume of the Philosophical Transactions.]

The process of birth is usually divided into several stages. The first comprehends the period extending from the commencement of the "pains" to the opening of the os uteri; the second reaches to the rupture of the membranes of the ovum. This takes place when, the os uteri having opened, a part of the membranes containing the liquor amnii are protruded through it in the form of a pouch; this pouch bursts and the "waters" escape. The third stage extends from the rupture of the membranes to the presentation of the head at the outlet of the pelvis. During this stage the head descends through the dilated os uteri into the vagina. In the fourth stage the occiput escapes from the external parts of generation, whereupon the other parts of the child follow, the shoulders entering the pelvis in the oblique diameter of its inlet, and leaving it in the antero-posterior diameter of its cavity. During the last stage of birth, the "after-birth," consisting of the placenta and the membranes of the ovum, is expelled. For after the birth of the child the contractions of the uterus continue; and in consequence of the part to which the placenta was attached becoming very much contracted, that organ is separated, an effusion of blood taking place from the torn vessels. The separation and expulsion of the placenta occur in from half an hour to an hour after the birth of the child; so that all the stages of delivery are completed in the space of six or twelve hours. When the after-birth is expelled, the uterus contracts still more closely.*

In animals the process of birth is in general attended with less difficulty than in the human species, both on account of the wedge-like form of the head of the fœtus, which is preceded in its passage through the pelvis by the fore-feet, and on account of the greater mobility of the os coccygis.† In the vampires the birth of the young is facilitated by the pubic bones not being united in the middle line in these animals, and in Cavia aperea and other animals by the symphysis pubis being capable of dilatation.

b. *The mother and child after birth.*

The child breathes immediately, and cries as soon as its respiratory organs are relieved from the pressure to which they were subjected during birth. The umbilical cord is tied and divided by the persons assisting at the labour. In brutes the umbilical cord generally becomes ruptured spontaneously during birth at a soft spot not far distant from the navel: in some cases it is bitten asunder by the mother. The umbilical vessels soon contract, so that their cavity is quite obliterated. During the first two or three weeks after birth, also, the foramen ovale in the septum auriculorum, and the ductus arteriosus Botalli become closed; and hence from this period all the blood sent to the body must pass through the lungs, and *vice versâ*; the pulmonary circulation now becoming a part of the general circuit which the whole mass of blood performs, whilst before merely a fraction of the blood in the general circulation traversed the lungs.

The newborn mammiferous animals instinctively seek the teats of the mother, and the newborn child also exhibits a constant impulse to suck every object which is offered to it.

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* See F. C. Naegele, Ueber den Mechanismus der Geburt, in Meckel's Archiv. t. v. 1819, p. 483. Hueter, im Encyclopæd. Wörterb. d. Med. Wiss. xiv. p. 44. Those readers who desire more full information respecting the process of birth and its variations, should consult the above treatises and special works on midwifery,—such as those of Carus, Stein, Busch, Kilian, Ritgen, and H. F. Naegele.

† See Stein, Unterschied zwischen Mensch und Thier im Gebären. Bonn, 1820.

In the maternal organism, during the first days of the puerperal state, the secretion of milk, which had shown itself in a slight degree during pregnancy, becomes suddenly increased, and the organic activity which was previously expended in the uterus is now transferred to the breasts; while all the maternal feelings at first expressed in the mother's joy at the birth of her living but helpless offspring, are concentrated in the fond office of nourishing and protecting the child. A bloody discharge in moderate quantity, the "lochia," flows from the female organs during some days after birth, and then is succeeded by a serous discharge which gradually, as the inner surface of the uterus regains its state of integrity, becomes a mere mucous secretion. The secretion of milk is excited in increased quantity by the mechanical irritation of the nipples during the act of sucking, and by all ideas of the mother relating to the nourishing and presence of the child. When once in existence, this secretion may often be maintained for a very long and indefinite period, as is observed in brutes, and sometimes also in the human female. Usually, however, it diminishes in quantity when the menstrual flux reappears about the ninth month. In women who do not suckle their children, the menstrual flux is generally restored at an earlier period, about the sixth week after birth.

The milk of pregnant women, and of puerperal women, immediately after birth, is called the "colostrum." According to the observations of M. Donné, it contains, besides the ordinary milk or flat globules, peculiar granulated corpuscules which may be detected in it until about the twentieth day after birth. The proper milk globules which give the milk its white colour consist principally of fatty matter; but they seem to be invested by a layer of some other substance, since they are not very readily dissolved by alcohol and ether. When milk is left at rest, the fat globules collect, for the most part, at the surface of the fluid and form the cream, which consists of the fat of milk or butter. When milk is subjected to continued agitation, the fat globules coalesce and form butter; and when this is removed, merely the fluid part of the milk remains. This fluid holds in solution the other components of milk,—namely the caseine, the sugar of milk, and the salts. The fatty matter of milk is one of those fats which are destitute of nitrogen, and convertible into soap.

The caseine is soluble both in warm and in cold water, and is not coagulated by boiling. It is precipitated by alcohol, corrosive sublimate, alum, and acetate of lead; the precipitate in every case being redissolved by water after the reagent has been removed by washing. Acids in small quantities precipitate the caseine; but when added in excess, they redissolve the precipitate. Pepsine and the rennet containing it exert a peculiar action on caseine: they precipitate it and at the same time render it insoluble in water. The ferro-cyanuret of potassium renders the solution of caseine in acids turbid, or precipitates the caseine. In respect of its elementary composition, caseine, and consequently milk, are to be ranked amongst the nutritive substances which abound in nitrogen. According to Mulder's analysis, it contains, in addition to a small proportion of sulphur (namely 0·41)—

Carbon	55·10
Hydrogen	6·97
Nitrogen	15·95
Oxygen	21·62

Both the other principal ingredients of milk, the fatty matter, and the sugar of milk, are destitute of nitrogen. After the separation of the butter and the caseine from milk, the sugar remains in solution. The sugar of milk crystallizes readily: when pure it is not susceptible of fermentation; but, under the influence of the azotised caseine, it appears to become changed into sugar of mucus. The composition of the sugar of milk, according to the analyses of Gay-Lussac, Thenard, Prout, and Berzelius, is as follows:—

Carbon	40·46
Hydrogen	6·60
Oxygen	52·93

Fresh milk of the human female is slightly alkaline; cow's milk, even when fresh, is sometimes feebly acid; but, when allowed to stand for some time, and especially when the atmosphere is in a state of electric tension, all milk becomes acid owing to the transformation of some of its components, probably of the sugar. The acid of sour milk is lactic acid.

The milk of different animals is not identical in all respects. Simon found that the caseine of the milk of the human female was not precipitated by acids. This was probably owing to the small quantity of the caseine contained in the milk, and the large quantity of acid added. For a diluted solution of caseine is not precipitated except by the smallest quantity of acid. A slight excess of acid redissolves the caseine.

The milk of the human female is, according to Payen, of the following composition:—

Butter	5·18	5·16 or 5·20
Caseine	0·24	0·18 or 0·25
Solid residue of the evaporated fluid of the milk	7·86	7·62 or 7·93
Water	85·80	86·00 or 85·50

Cow's milk, from which the cream had been removed, was found by Berzelius to contain:—

Of caseine, with a portion of the fatty matter	2·600
Sugar of milk	3·500
Alcoholic extract, lactic acid and its salts	0.600
Chloride of potassium	0·170

Alkaline phosphate	0·025
Phosphate of lime, free lime combined with caseine, magnesia, and traces of oxyde of iron	0·230
Water	92·875

The specific weight of human milk is from 1·020 to 1·025; that of cow's milk 1·03.*

CHAPTER II.

OF THE DIFFERENT AGES OR PERIODS OF LIFE.

PROCESSES of development continue to be in operation after birth through a great part of life, although they are of a less important nature than those perfected in the fœtal state. It is only in a few classes and orders of animals which undergo metamorphoses, (as the Insecta, some Crustacea, the Cirrhopoda, the Hydrachinda amongst spiders, and the Amphibia amongst Vertebrate classes,) that fundamental changes of form, and the new development of organs and groups of organs, are observed after the termination of embryonic life. The changes of development which occur in the higher animals and man after birth are limited to certain modifications of form, &c., which mark the different ages or periods of life. Adopting that division of the life of a human being which is defined by the most remarkable processes of development or by their completion, we may distinguish the following ages or periods of life.

1. *The period of embryonic life.*—During this period the processes of formation and growth are in their greatest activity. The organs which are being formed present none of their functional phenomena, or only the gradual commencement of them. In the Amphibia there is no distinction of sex during embryonic life; in fact, the organs of generation are not formed. These organs are developed in the larva a considerable time after its escape from the ovum. In the rest of the Vertebrata, however, the distinguishing marks of the sexes become manifest during embryonic life. The causes which determine the sex of the embryo are unknown, although it appears that the relative age of the parents has some influence over the sex of the offspring.† In animals which bring forth many young at a birth, one act of coitus produces both males and females, and in those animals in which the

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* See Donné, Du lait et en particulier de celui des Nourrices. Paris, 1837. Müller's Archiv. 1839, p. 182. Henle, Froriep's Notiz. 1839, p. 223. Simon, die Frauenmilch. Berl. 1838. Marchand im Encyclop. Wörterb. d. Med. Wissensch 23 Bd. p. 309.

† See Girou de Bouzareingues, Ann. d. Sc. Nat. t. xi. pp. 115, 314; t. xiii. p. 134. Hofacker, De qualitat. parent in sobol. transeunt. Diss. præs. Tubing, 1827; and Heusinger, Zeitschrift für. org. Physiol. t. ii. p. 446.

impregnation of the ova is effected out of the body, the same seminal fluid fecundates ova which yield young of both sexes. But how different soever the proportion of the sexes in different families, in larger numbers they always bear an equal proportion. The law which effects this equalization of the numbers of the sexes is in operation in each individual of the species. The equalization of particular deviations from the general proportion is the result of an original provision, just as is the balance of the gain and loss, or of the "even" and "odd" in lotteries or any game of chance which is governed by a general law.

2. *The period of immaturity.* — This period extends from birth to puberty. It is marked by growth, by the development of the forms of the different parts of the body, and by the gradual perception and analysis, by the mind, of the different phenomena of the senses. Several local phases of development occur in this period; for example, in the human subject the first irruption of the teeth, beginning about the middle of the first year after birth, and the displacement of the temporary teeth by the permanent set, which commences in the sixth year. The changes of development afford a basis for the establishment of a period of childhood, extending to the sixth year; and a period of boyhood, reaching to the fourteenth or fifteenth year. In the former of these periods the necessity for nourishment is greatest, the changes of material which the organs suffer is more rapid and greater in degree, and the quality of the food is consequently now of the greatest importance. Hence, in childhood, the organs frequently become affected with various defects of material composition, or defects which are maintained by improper food being given. Such are the diseases called mollities ossium, scrofula. When the period of boyhood commences, the mind has acquired the capacity and strength required for the accumulation of knowledge and for its own cultivation; the process of growth now progresses less rapidly; and the organs of the body receive their permanent material composition. This is the age occupied by education and mental culture, when the foundation is laid in which all the future operations of the mind have their root.

3. *The period of maturity* begins at puberty and ends at the period when the generative power is lost, which in woman occurs about the forty-fifth or fiftieth year. The period of maturity may be subdivided into the ages of youth, and manhood or womanhood. While the changes of development more especially characterising puberty, and already described, take place, the organs of respiration and voice (as has been mentioned in the section on the voice) undergo a further development, and the external form of the different parts of the body is perfected; the features at this period frequently undergoing a very rapid change and taking that character which they afterwards retain throughout life. The previously boyish countenance now serves to express more vio-

lent passions; the leading influence of others ceases and is no longer tolerated; the tricks of the child are cast off, and the errors of the youth who has become independent, who trusts to his own experience and feels himself free, begin to manifest themselves. The corresponding changes take place earlier and more rapidly in the female organism, and hence the girl deserts the games still followed by boys of equal age upon whom she looks down with contempt, though when they also have passed the period of puberty she is timid and bashful in their presence. In both sexes the imagination is now most active; this is the period when the mind is most under the influence of a poetical fancy, when it is devoid of envy, avarice, and jealousy, and is filled with open disinterested friendship. A boundless field of action and meditation is in prospect. The limits to his capabilities of which the serious, cold man becomes conscious, are yet unknown. Love is the centre of the most noble feelings. The vegetative development as far as it regards the individual is now complete, and the increase of the organic force is applied to the new products of the generative function. Those individuals in whom the formative and equalizing power was at first unstable and the material composition of the organism defective, already manifest an inability to resist the action of external stimuli, particularly when these are applied to such important organs as the lungs; for the lungs at this period, on account of the increased development which they are undergoing, possess an extraordinary degree of irritability. Hence when the system has undergone the changes of puberty there frequently appears a predisposition to pulmonary disease which had previously remained latent during the active growth and development of the different parts of the body, just as hectic frequently ceases during pregnancy.

While the body continues to grow, the epiphyses of the bones remain separated from the diaphyses by sutures; the elongation of the bones taking place at these points. When the individual has attained his full stature, the epiphyses become united to the diaphyses by ossification.

In the age of manhood the slim forms of youth frequently give place to greater bulkiness and obesity of figure, which manifests a failing influence of the formative power over the masses of the body. At this period of life also the mind has attained its maturity, has laid aside the exuberance of the feelings, and is conscious of efforts made, of endeavours miscarried, of the limits of its faculties and of the feeling of possession; life has become more tranquil; the views of the individual are more clear and more serious; he still has his passions, but they are active in another direction, in the acquisition of possessions and in self-defence.

Within the age of manhood there is no predominant disposition to diseases of particular organs. Yet in advanced manhood the morbid changes by degrees manifest a preference for those organs which are chiefly engaged in impressing chemical changes on the matters submitted to their influence, for example in the large glandular viscera; and the weakened vegetative power is the less able to resist obnoxious agencies the more frequently they are excited. It is not the lungs which now suffer; after the excitement which they experience in youth those organs gradually regain a state of repose. The organs of the abdomen are now especially subject to the abnormal changes; whilst the effects of foregone disturbances of the nervous system are more perceptible and more enduring than in youth when the foundation for them possibly was laid. The age of manhood is moreover particularly prone to mental diseases owing to the intensity of the shocks to which the mind at this period of life is subject.

4. The last great period of life may be designated the *period of sterility*. It extends from the cessation of the fruitful exercise of the generative function to extreme old age. The form of the body now loses its plumpness and "turgor." The growth of the hair which began on the head, and, subsequently, in the periods of youth and manhood, extended to the face, ceases also first on the head and continues to extreme age only in the beard. In old age also there is manifested a tendency to the deposition of calcareous salts in the cartilages and coats of the blood-vessels. The teeth or their remains lose their firm attachment to the jaw-bones, and after they have fallen out, the alveoli disappear. Hence the jaw-bones in old age become shortened. In this period of life, when all the development is at an end, there is a more or less uniform diminution in the energy of the different vital functions, while the intensity of the propensities, inclinations, and sympathies, the acuteness of the senses, the liveliness of the fancy, and the spirit of self-defence and resistance fail. Very few individuals reach an age in which this diminution of the faculties leads imperceptibly to the close of natural life. In most persons the foundation of premature decay is laid in local causes. But even independently of this circumstance the organism in old age after all the processes of development are completed bears a stronger resemblance to a piece of artificial mechanism than does the primary form of the organic being which generates the mechanism of the body out of its own mass, and therefore can make good the lesions which it may suffer. In old age a slight disturbance produced by an external cause is capable of arresting the whole mechanism.*

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* The subject of the different ages of man's life is treated of very fully in the third volume of Burdach's Physiologie.

CONCLUDING REMARKS ON THE VARIETIES OF MEN AND ANIMALS.

From this review of the process of development of the individual animal organism, we are brought back again to the contemplation of the general forms to which the individuals belong as examples of species or genera; and thus the conclusion of the "Special Physiology" connects itself with those considerations which were discussed in the "Prolegomena on General Physiology." The races of animals and plants suffer modifications under the various conditions to which they are exposed in their distribution over the surface of the globe. These modifications do not exceed the limits marked out by species and genera, but they are perpetuated as types of "varieties" of the species through successive generations. It is to these phenomena that our attention must now be directed.

It is important in this inquiry to attach definite ideas to the terms "species" and "variety." The species is a living form represented by individual beings, which reappears in the product of generation with certain invariable characters, and is constantly reproduced by the generative act of similar individuals. The latter character distinguishes the species from hybrid forms. It is not an exclusive character of the living form which we denominate species, that one form produced by generation is capable of productive union with another individual: this character is inadequate to mark the two individuals thus propagating as belonging to one species. For individuals belonging to two different species of one genus are likewise in some instances capable of propagating with each other, as in the cases of the dog and wolf, and the horse and ass, where mules or hybrids are produced. The type of the genus, represented by different species, and individuals, is alone incapable of a fruitful union with individuals of species belonging to another genus. But hybrids, the production of which is rendered infrequent by the natural repugnance of the individuals of different species to generative union, cannot propagate their distinguishing characters by generation. The sexual union of hybrids is generally unfruitful; and when fruitful, as in the case of the union of a hybrid with an individual of one of the species which had co-operated to form the hybrid, the product relapses into the type of one of the original species. The constant reproduction of the same form by the sexual union of similar individuals is therefore an invariable and essential characteristic of the species.*

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* Consult on this subject Rudolphi, Beiträge zur Anthropologie und allgemeinen Natur-geschichte. Berlin, 1812. Prichard, Natur-geschichte des Menschen-geschlechts. Leipz. 1840, p. 174. [Physical History of Man, London,] translated into German by Rudolph Wagner; and also the notes of Wagner in the same work, p. 439.

" Varieties" are forms represented by individuals but included within the definition of the species. The individuals constituting one variety are capable of fruitful union not only with each other but also with individuals belonging to other " varieties" of the same species. Individuals belonging to different genera are not capable of fruitful union; and individuals of different species can propagate with each other, but their products cannot reproduce their peculiar form by generation; varieties have both these faculties. The mixed race produced by the union of two races is capable of propagation by union with similar individuals; but the union of the mixed race with the original race which had concurred in its production yields an offspring which in successive generations approaches more and more nearly to the type of the unmixed races. These characters sufficiently distinguish the " variety" of a species which when permanent, is a " race." The variety may however be otherwise defined and distinguished from the species. The different species always remain distinct. The races composing them present no stages of transition of one species into another. Where different forms of animals exhibit this gradual transition of the one into the other, they cannot be regarded by the zoologist as distinct species. With the " variety" the case is otherwise. There is a remote possibility that the similar productive individuals of one variety of a species, or a race, inasmuch as they contain within themselves the essential properties of the species, might produce all the other varieties of the species, provided the internal and external conditions necessary thereto were in action during a long series of generations. But there is no remote possibility of one species being produced from another. All the phenomena at present observed in the animal kingdom seem to prove that the species were originally created distinct and independent of each other. While the different varieties of each species may be accounted for by supposing the original existence of a pair of individuals of opposite sexes belonging to the same species, and the constant action of different external modifying agencies, such as that of climate, upon several or many successive generations.

The causes which give rise to the varieties of species are partly seated in the organisms of the animals themselves, and are partly external conditions,—such as the food, the elevation above the sea, and the climate. Each species of plants and animals possesses within itself a power of variation within a certain limit, quite independently of any external influences. To this cause are to be referred the varieties of form which may present themselves in the offspring of one act of generation. In each individual of a species there is an innate capability of producing such varieties as these, since each individual of a species does not produce by generation the mere repetition of itself, but generates new beings in accordance with laws which regulate the whole species. Thus from the same parents there may be produced individuals with fair and others with dark hair; some of spare and slender figure, and others of plump and stout robust form; individuals of different temperaments, and with different features, eyes, mouth, and nose, with hair in some instances curly, and in others straight. The most common varieties arising in this way from internal causes, are the fair and the dark haired. Fair persons are occasionally met with amongst races for the most part characterised by black hair,—for example, amongst the Mongolians; and Dr. Prichard adduces several examples of fair-complexioned negroes who were not albinos.

It is true that these varieties are chiefly due to the parents being individuals of different complexions, and to the characteristics sometimes of one and sometimes of the other being predominant in the offspring. But even when the parents have the same complexion, a certain variety of forms and internal properties may present itself in the offspring. In consequence of the mingling of these different varieties in marriage, their peculiarities are not preserved, and are not propagated as constant fixed types. It is easy to conceive the conditions which must be combined in order, independently of climate, food, and locality, to convert these accidental varieties into persistent types. The longer individuals of the same stock continue to unite in marriage, without foreign admixture, the longer will the type to which they belong be preserved. In this way, and independently of all external influences, a race will be formed. Sometimes when the type has become fixed through a series of generations in the members of a family, even the admixture of a foreign type is not sufficient to efface the fixed characters of the family, and the foreign element becomes lost in the older fixed type. Hence we see in many royal families that in spite of their union by marriage with other houses, the type of the family features is in a remarkable way preserved and transmitted from generation to generation,—as, for example, in the Bourbon family, and equally in many princely houses in Germany. It was previously shown how one family, being isolated by the intermarrying of its members exclusively with each other, might produce a nation or tribe with general distinguishing characters. History teaches us how the national type once formed is preserved in spite of individual variations through thousands of years, and that, except when modified by admixture with other types, it is maintained unchanged, as in the case of the Jews, even in the most varied climates which produce their peculiar modifications of form and complexion.

The propagation of like with like is, however, capable of perpetuating, not merely a physical type forming one of the varieties of a species, but also the faculty which individuals acquire by education. The peculiar properties of the hound, the shepherd's dog, and the watch-dog, for example, all are comprehended in the general notion of the species; and it is probable that in the brood of a single wild dog, or in the generations descended from this brood, through the inherent tendency of the species to the production of varieties, individuals occur which, when tamed, discover very different talents,—the one being more adapted for the chase, another for tending of sheep, and a third for keeping watch or guarding property. But the education and rearing of the dogs with the requisite endowments for the purposes mentioned, cause the faculties thus improved or acquired to be transmitted to succeeding generations, when this object is provided for by the pairing of males and females with similar endowments.

Varieties of species are also produced by external influences; and the longer the action of these causes is continued, the more constant does the particular variety become, and the more does it acquire the character of a type. To these external causes belong the climates or zones in which the animals live. The warmth or coldness of the climate has an especial influence on the fur or hairy coat of animals. Most animals, as is well known, have two kinds of hair in their coat,—namely, long and stiff hairs, and between these a shorter, curly, woolly hair. Now, the further a sheep is carried towards the north, the more equal does the proportion of the two kinds of hair in the coat become; while in sheep living in southern countries the woolly hair increases in quantity at the expense of the stiffer, longer hair. This is exemplified in the merino sheep inhabiting the mountains of Spain. Climate modifies also the "habitus" and size of animals. Cattle transported from the temperate zones of Europe,—for example, from Holland or England to the East Indies,—are said to become considerably smaller in their succeeding generations.* On the other hand, the skin of the cattle carried to South America has in a series of generations gradually become so much changed in its properties, that the Brazilian hides now supply the best leather. The guinea-pig, Cavia aperea, which in its native country is of a grey colour, since its introduction into Europe has become changed into a variety marked with brown, black, and white spots. The elevation of the locality above the sea also, independently of the degree of latitude, has an influence over the forms of animals. According to Sturm, the hog in low countries or districts,—as in East Friesland,—attains the greatest size of trunk, with long and deep flanks, but with short legs. While in proportion as the country which the hog inhabits is elevated above the level of the sea, the smaller and more compressed becomes its body, the less tapering and shorter its head; the shorter and thicker its neck, and the more rounded its hind quarters. But the food also modifies the form and nutrition of animals; hence in the low countries of Holland, East Friesland, and Holstein, the cattle are remarkable for their large size, and for the abundant supply of milk which they yield, while they are defective in both these qualities in barren Iceland.

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* See Sturm, Über Racen, Kreuzung, und Veredlung der landwirthschaftlichen Hausthiere. Elberfeld, 1825, p. 54.

The concurrence of different conditions of internal as well as external nature, which cannot be severally defined, has produced the existing races or fixed varieties of the different species of animals; the most remarkable of which varieties are to be met with in those species which are susceptible of the most extended distribution over the surface of the earth.

The principal modifications, in addition to those of external form, are to be found in the skin, in the coat, the horns, and the adipose deposits. Sometimes the ears are lengthened and become pendulous,— as in the Kirghisic sheep, and some varieties of the dog; sometimes the horns are wanting, — as in the English sheep, or are spirally twisted, — as in the Hungarian sheep; sometimes the adipose tissue is accumulated in the form of a hump on the back, — as in the little zeburind, or in the tail,—as in the sheep of Thibet and the bucharei; sometimes the hair of the coat is curled, as in the poodle-dog, or forms a very thick wool, as in the merino sheep. In the human species also prolongations of the skin, varieties in its appendages, and local accumulations of fat occur in different races; for example, the elongation of the nymphæ and their commissures in the Hottentot females and the females of the Bosjesman or Bushman race; the straight hair which may be abundant or scanty, the curly hair and the woolly crisp hair, and the accumulation of fat about the buttocks and sacrum of the Hottentot and Bosjesman females.

The modifications in the form of the species produced by the influence of climate are seldom so deeply rooted, that they are not gradually lost when the climate is changed, and then they may be replaced by the peculiarities produced by the new climate. Thus the wool of merino sheep, imported by Englishmen into some of the South Sea Islands, has soon become changed into straight hair. The wool of the same variety of sheep, when they are transported to Peru and Chili, very soon gives place to straight stiff hair.* A German gardener repeatedly imported the seeds of the white cabbage from Germany into Naples in order to rear heads of cabbage which at the latter place were still unknown; but he always failed, for he could raise only leafy cabbage, or the cauliflower variety. According to Sturm also, the Siberian naked barley, Hordeum cæleste, when grown on the Rhine frequently degenerates into common barley.

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* Sturm, op. cit. p. 42 and 50.

There are, however, examples of typical varieties produced by influences connected with climate, which have not lost their peculiarities in successive generations when transplanted to a different climate, provided the preservation of the type has been favoured by the individuals of the variety constantly propagating with each other. The different races of mankind afford the most striking examples of this fact.

The races of the human species answer to the general notion of a "race;" they are different forms of one species which are capable of fruitful union, and are propagated by generation: they are not different species of one genus; for were that the case their hybrids would be unfruitful. Here, as in the case of other animals, all the varieties are to be regarded as aberrations from one type, caused partly by differences in the progeny of the same parents maintained by repeated propagation of similar forms with one another, and partly by the external influences connected with climate. Whether the first individuals of the species were originally placed in different parts of the globe at the same time, or whether they existed originally in one spot, and have spread themselves thence over other parts, is a question not affecting this statement. Some of the extreme forms of the races of mankind are certainly varieties which are no longer produced anew with all their distinguishing peculiarities, either by internal causes, or by the influences of climate, and which lose their characters in no climate, but propagate them in all their purity when foreign admixture is avoided. For negroes in the temperate and colder climates remain black, and retain all the characters of negroes, and also by generative union with each other produce only negroes; whilst Europeans in hot climates, except that the colour of their skin becomes somewhat darker, retain the characters of the European race. Under the same degrees of latitude negroes, Europeans, and the copper-coloured American Indians retain their respective forms and colours; and on many of the Australian islands there are found natives with all the characters of the Malay race, and with them black men of the negro variety. Yet even these races are not so absolutely distinct that the innate tendency to variation does not determine in one race individual cases of approximation to another, and that the same does not happen from the influences of climate. Individuals of the European race sometimes have hair nearly as crisp and woolly as that of negroes. The negro form of the face and head likewise occurs in individual cases amongst the Europeans. Weber states, that besides the ordinary oval form of the skull, there may be found amongst European skulls of the elongated and quadrangular forms which are to be regarded as instances of sporadic approximation to the negro and mongolian types. The differences in the form of the pelvis in different races have been much elucidated by Vrolik. The form of the pelvis is sometimes very different from the ordinary European type, and particularly in the negroes and

Bosjesmans, in whom the vertical position of the iliac and other characters indicate an approach to the form of this part of the skeleton in brutes. But in the form of the pelvis also the different races present aberrations from their proper type. According to Weber's researches there are in every race examples of pelves with the inlet of the oval, the round, the quadrilateral, and the wedge-like form. In the negro race there are many aberrations from the general type, such as the brown-black colour of the Hottentots and Bosjesmans, the only half-woolly hair of the Papuan negroes of Australia, the coalescence of the ossa nasi into one bone, which sometimes occurs among the Hottentots and Bosjesmans, and the elongated nymphæ of those tribes. Moreover, although the action of light and the temperature of different climates on the skin is extremely various in different races and nations, yet their influence is to a certain extent evident in all races ; in all the skin is more or less darkened by residence in hot climates. This susceptibility to the action of light and heat is greatest in the negroes ; so that the child, which during its embryonic existence was white, becomes coloured by exposure to the light after birth. In Europeans of fair complexion the skin does not become darkened from exposure to the light, which it does in Europeans with dark hair.

The question whether the different races of mankind all derive their origin from one parent stock or from several stocks, can never be determined by practical observation. But this question is not so important in reference to the theoretical explanation of the races, as some physiologists have supposed. For whether many or a few individuals of an animal or plant were created at the same time, still the conditions which give rise to the varieties would exert their influence on individuals. The history of the races of animals and plants conducts us inevitably to the conclusion that all the true varieties of one species may be produced by the action of internal and external causes through a sufficiently long period of time on individuals of the species.

It is impossible to make a strict division and classification of the races of mankind. For the various forms do not possess equally marked peculiarities, and there is no such sure, scientific, intrinsic principle to guide us in defining their limits, as there is in the case of the species. The object of a physical history of man is to describe all the peculiarities of the nations which maintain themselves distinct by the successive generations of each not mingling with those of the others; but the contemplation of mankind in this extended manner does not come within the scope of this work. All that is here practicable is to enumerate the most conspicuous of the races of mankind according to the arrangement proposed by Blumenbach, which is still preferable to all others, because it is the most convenient.

The races distinguished by Blumenbach are :—

1. The *Caucasian race.*—In this race the colour of the skin is more or less white, passing into flesh colour; more rarely it is of a light brownish colour. The hair is more or less wavy, and of a light or dark tint. The forehead is high and arched; the face oval; the facial angle * large, namely, from 80° to 85°. The nose is slender, more or less arched or prominent; the teeth perpendicular; the lips of moderate thickness; the chin prominent; the beard abundant; and no scantiness of the growth of the hair of the surface generally. To this race Blumenbach assigns the Europeans (with the exception of the Laplanders and Finns) the inhabitants of Western Asia, as far as the Obe, the Ganges, and the Caspian Sea, and also the North Africans.

2. The *Mongolian race.*—The characteristics of the Mongolian variety are a yellow complexion; black, straight, scanty hair; a broad, flat face, which is widest where the cheek-bones project; a flat and broad glabella (the space between the eyebrows); a short, broad, and flattened nose; narrow and oblique openings of the eyelids and eyes, placed wide apart.

To this race Blumenbach refers all the Asiatics not belonging to the Caucasian variety, except the Malays; the Laplanders and Finns in Europe; the inhabitants of the most northern parts of America, the Esquimaux and Greenlanders.

3. The *American race* has a brownish copper-coloured skin; black, straight, scanty hair; a beard more or less feebly developed; a nose more or less prominent. All the other characters assigned to this race are neither constant nor striking.

This race comprehends all the Americans not included in the preceding variety.

4. The *Ethiopian race.*—The characters are a black or a brownish black complexion; black, generally coarse, short, woolly, and frizzly

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* By the facial angle is understood the angle included between the facial line and a horizontal line drawn from the base of the cranium. The former of these lines touches the glabella or space between the eyebrows and the most prominent part of the superior maxilla beneath the nose; the latter line is the middle line of a plane passing through the anterior nasal spine of the superior maxilla and the meatus auditorius externus. This angle is always larger in children than in adults. In the same way, it is proportionally large in young apes, as in the young ourang, while in full-grown apes it is much smaller, and the face has consequently a more brutish character. The size of the facial angle is determined by the proportion borne by the cranial portion of the head to the parts occupied by the senses and those engaged in mastication and the taking of food. In the antique sculptures this angle is enlarged to the extent of a right angle, and still further, in order to give a more noble expression to the head, and hence in this point the form of the child is transferred to the adult. According to the researches of Tiedemann the capacity of the cerebral cavity of the cranium is the same in different races of men, how different soever the external forms of the skulls may be. See Tiedemann, Das Hirn des Negers mit dem des Europäers und Orang-utans vergleichen. Heidelberg, 1837, p. 4.

hair; a narrow and long skull; a retiring forehead; a prominent upper jaw with a retiring chin, and teeth projecting obliquely; a small, turned-up nose, compressed above; thick lips; and a facial angle of only 70° to 75°.

All the inhabitants of Africa, except those belonging to the Caucasian variety, namely, the African negroes, and the negroes of New Holland and the Indian Archipelago, or the Papuas, constitute this race.

5. *The Malay race.*—The skin is black; the hair black, soft, curling and abundant; the cranium moderately narrow; the forehead arched; the upper jaw moderately prominent; the nose short and broad; the lips thick, and the mouth wide.

To the Malay race belong the brown islanders of the South Sea; the inhabitants of the Sunda Isles, the Moluccas, the Philippine and Marianne Isles, and the true Malays of Malacca.

It would, doubtless, be more consonant with nature to regard these races as constant and extreme forms of the varieties of mankind, than to endeavour to make them include all the nations of the earth, a task which is impracticable, and which science does not require to be performed. The attempt to effect such an arrangement of all the varieties of mankind under one or other of these classes inevitably leads to an arbitrary classification. The position of the Tartar and Finnish tribes in relation to the Mongolian and Caucasian races is quite uncertain, and they cannot be referred to either exclusively except by a mere arbitrary decision. The same remark applies to the Papuas and Alfouros in regard to their classification with the Malays or with the negroes. Amongst the islanders of the Pacific both black and brown and even white men may be distinguished; at all events, in the Society Isles there are white natives as well as those of a yellowish brown complexion. In this case the whites cannot be referred to the Caucasian race, any more than the idea can be entertained of classing the Guyacas of America with the Caucasian race on account of their light complexion. On the contrary, these varieties seem to have arisen among those nations in the same way as the fair and dark complexioned varieties have been produced among Europeans. But it further admits of inquiry whether the Papuas and Alfouros should not be regarded as distinct from the African negroes in their origin, and whether these black races of the Indian Archipelago are not, on the contrary, much more nearly related to the brown Malay race, in which case these blacks and the brown Malays might be supposed to stand in the same relation to each other as the true negroes and the dark brown inhabitants of Southern Africa. No necessity exists for deriving all the black people on the globe, or all the brown or all the white races, from the sameroot; on the contrary, since we have seen that varieties may arise among the progeny of one stock, it is easy to conceive how it is possible for nature to produce similar forms in nations which are far removed from each other, and according to the records of history have never mingled.

Similarity or difference of language may sometimes aid us in determining the relation borne by a particular people to the principal races of mankind; but even this criterion is not always trustworthy, for not unfrequently languages sprung from very different roots are met with amongst the people of one race. Languages, like races of men, perish and are displaced by others.

With respect to the original roots of languages, there may be distinguished upon the great continent of Europe and Asia—

1. The nations whose languages are derived from the Indo-European root; these languages are the Sanscrit, the Persic, the Greek, the Latin, the German Celtic, and the Sclavonic Celtic.

2. The nations speaking the Semitic tongues, namely, the Aramæic, Phœnician, Hebrew, Arabic, to which must be added the Aethiopic or Geezic in the Northern and North-eastern parts of Africa.

These are the nations of which the most perfect history has been preserved, and who have in the greatest degree been susceptible of civilization. The same nations are comprehended under the name of the Caucasian race.

3. The nations using the Tschudic tongues, to which are referred the languages of the Hungarians, Finns, Laplanders, Samoyedes, Esthonians, Livonians, Permiens, Wogules, Ostiakes, Cheremisses, Mordwines, Koriakes, Tchuktches, and Kuriles, and, by some writers, the languages of the nations of the Caucasus, as the Georgians and the Circassians.

4. The nations speaking the Tartar or Mongolian tongues, as the Mantchoo in China, the Turkish, and the dialects of the Usbecks, Bucharians, Bashkires, Yakutes, Kirghises, Calmucks, Tungooses, &c.

5. The nations having monosyllabic tongues, partly languages of symbols, as those of China, Tonkin, and Cochin China; partly languages with syllabic alphabets, as those of Thibet, Siam, and Birma. These languages have no inflections, and express the relations of words by means of intonation.

Australasia is inhabited partly by brown Malays, partly by the brownish black Papuas and Alfouros. The Alfouros live in the central parts of most of the Moluccas and Philippine Isles of Madagascar and New Guinea, also in the North of New Guinea, of New Britain, New Ireland, Louisiade, Bouka, Santa Cruz, Solomon's Islands, and are scattered through the interior of New Holland. They are regarded as the original inhabitants. M. Lesson describes them as having thin legs, prominent teeth, rough, thick, straight hair, a thick beard, and a dirty brown or black complexion. The Papuas, who are a different variety and live on the coasts, call the Alfouros Endamines. The Papuas who live on the coasts of many islands in the Malay seas, appear to be a mixed variety between the Malays and the Alfouros or true Papuas, and resemble the inhabitants of Madagascar. Their hair is moderately woolly, thick, and long; their nose is flat, the nostrils dilated transversely, the forehead high, the beard thin, and their colour a deep black brown.

The Malays have spread themselves from Sumatra over the peninsula of Malacca; and here also are found the tribes of both colours in the mountainous districts, namely, besides the true Malays, the Samang tribes, woolly haired Negritos.

Malay dialects nearly allied to each other are spoken in the Philippine and Sunda Isles and in Madagascar. Of similar construction and composed of similar words are the languages spoken in New Zealand, Tahiti, the Sandwich Islands, and Tonga.

Africa is inhabited by two races. In the Northern and North-eastern parts dwell the Abyssinians, Nubians, Egyptians, and Berbers, nations allied to the Indo-Europeans. All the rest of Africa is occupied by negroes. The number of languages spoken is immense, and the same is the case in America, all the inhabitants of which continent, except, perhaps, the (Mongolian) tribes of the North-eastern part, appear to be allied to each other, notwithstanding the national distinctions of Peruvians, Guaranians, Araucanians, Pampas, Puris, Botocudos, Moluchas, Patagonians, Fuegians, Mexicans, Caribeans, Canadians, and Californians.*

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* The works treating specially of the Natural History of Man, are, Blumenbach, De generis humani varietate nativa, Gott. ed. iii. 1795; Blumenbach, Decades collectionis craniorum, Gott. 1790; P. Camber, Über den natürlichen Unterschied der Gesichtszüge in Menschen verschiedenen Gegenden und verschiedenen Alters, Berlin, 1792; Virey, Hist. Nat. du genre humain, Paris, 1824; Desmoulins, Hist. Nat. des races humaines, Paris, 1826; Bory de St. Vincent, Der Mensch, Weimar, 1837; G. Vrolik, Considérations sur la diversité des bassins de différentes races humaines, Amsterd. 1826; J. M. Weber, Die Lehre von den Ur- und Racenformen der Schädel und Becken des Menschen, Düsseldorf, 1830; R. Wagner, Naturgeschichte des Menschen, Kempten, 1831; Van der Hoeven, in Tijdschrift voor naturlijke geschiedenis, T. i., v.; die Menschenracen in der Deutschen Vierteljahrs-schrift, 1838; Prichard, Naturgeschichte des Menschengeschlechts (Physical History of Man), mit Anmerkungen und Zusaetzen von R. Wagner, Leipz. 1840; Berthold, Menschenracen, im Encyclop. Wörterb. d. Med. Wissensch. B. xxiii. p. 44. [Mr. Lawrence's Lectures on Man; and Morton's Crania Americana, Philadelphia, 1839.]

ERRATA.

Page 102, edit. i. or page 116, edit. ii. In the table showing the size of the red particles of the blood in different vertebrate animals, the measurements ascribed to the red particles of the "cat" and those of the "goat" require correction. They should be for the "cat" $\frac{1}{4286}$ of an English inch,

for the "goat" $\frac{1}{6469}$ " " "

Page 165, line 24, edit. i. ; *for* "which is most dense internally," *read* "which is most dense externally."

Page 201, line 17, edit. ii.; *omit* the comma after "lungs" and the words "the experiments on the production of respiration in hydrogen."

Page 374, lines 5 and 6, edit. i.; *for* "That this is not always the result is proved by the following interesting experiment, which Dr. Sharpey has kindly given the translator permission to mention," *read* "The following experiment, which Dr. Sharpey has kindly given the translator permission to mention, is interesting."

Page 490, line 17, edit. i.; *for* "nilghau," *read* "hippopotamus."

Page 882, line 16; *for* "about $\frac{1}{197}$ of an English line," *read* "about $\frac{1}{971}$ of an English line."

RECENT ADVANCES

IN THE

PHYSIOLOGY OF GENERATION,

OF THE UNIMPREGNATED OVUM.[*]

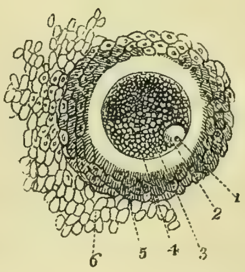
The observations of Bischoff and other inquirers relative to the structure and anatomical relations of the unimpregnated mammiferous ovum, which have been published since the commencement of 1842, have, for the most part, only confirmed the accuracy of results previously obtained. In a few instances, however, they have served to correct erroneous views or to settle questions which were before disputed.

It is well known that the ovum, when mature, lies at that part of the Graafian follicle which forms a prominence on the surface of the ovary, and is imbedded in a thickened portion (discus proligerus) of the layer of nucleated cells (membrana granulosa of Baer) which lines the follicle. The statement of Dr. Barry that the ovum is retained in this position by a peculiar apparatus, called by him the retinacula, has received no confirmation. Bischoff[†] expressly declares that he has never seen anything resembling such a structure.

Some recent observations on the intimate structure of the coats of the *Graafian follicle* will be detailed at page 53.

The *parts composing the ovum* are, 1. the external thick transparent tunic, known as the zona pellucida; 2. the yolk; and 3. the germinal vesicle with the germinal spot (see fig. 2). The investment of the ovum external to the zona pellucida, which Dr. Barry named tunica granulosa has no existence as a distinct and independent structure. It consists merely of an adhering layer of the cells belonging to the membrana granulosa in which, as has just been stated, the ovum is imbedded.

Fig. 2.[‡]



The doubt whether the *zona pellucida* be really a solid, transparent, structureless membrane, or a layer of albuminous fluid enclosed between two thin membranes, seems now to be resolved. Wagner,[*] Bischoff,[†] Henle,[‡] Barry,[§] and Wharton Jones,[||] all adopt the former view respecting the nature of this part.

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[*] Book vii. sect. ii. chap. iii. p. 1464 of Müller's Physiology.

[†] Entwickelungs-geschichte der Säugethiere und des Menschen. Leipzig, 1842, p. 10.

[‡] Ovum of sow, after Barry. 1. Germinal spot; 2. Germinal vesicle; 3. Yolk; 4. Zona pellucida; 5. Tunica granulosa of Dr. Barry; 6. Adherent granules or cells.

It is still, however, a disputed question whether internal to the zona pellucida there is not a second membrane enclosing the mass of yolk. Dr. Herman Meyer has stated[¶] that after he had completely dissolved the zona pellucida of an ovum, by the agency of a solution of potash, he ruptured the yolk, and allowed the yolk-granules to escape, and then saw a thin granulated membrane remaining, which had formed the proper investment of the yolk. Bischoff, however, has repeated this experiment, and affirms that in ova of the sow, cow, bitch, and rabbit, solution of potash does not dissolve the zona pellucida, but only produces contraction and condensation of it.[**] Meyer's observation seems, therefore, to have been an erroneous one; and as the membranes of which Dr. Barry has described[††] the successive formation and disappearance on the interior of the zona pellucida, cannot be regarded as constituting an essential part of the ovum, all proof of the existence of any membrane internal to the zona pellucida, derived from actual observation, fails. Wagner[‡‡] infers that such membrane exists, from the fact that an interval can sometimes be seen between the zona pellucida and the yolk, and that the latter has then a very defined outline. But Bischoff,[§§] as we shall presently see, gives a different explanation of this appearance, and denies positively that there is any other membrana vitelli than the so-called zona pellucida. Wharton Jones,[||||] Coste, and Henle entertain the same opinion.

The *yolk* is described by Henle[¶¶] as being composed of granules and globules of different sizes, imbedded in a more or less fluid substance. The smaller granules, which are the more numerous, in their appearance as well as their constant motion, resemble pigment granules. The larger granules or globules, which have the aspect of fat globules, are in greatest number at the periphery of the yolk. The number of the granules is, according to Bischoff's observations, greatest in carnivorous animals. In the human ovum their quantity is comparatively small.

The substance that combines the globules and granules of the yolk is, in many animals, quite fluid. The yolk then completely fills the cavity of the zona pellucida, and escapes in a liquid form when that membrane is ruptured: but in ova of the human subject and some other animals the yolk is much more consistent, and sometimes escapes as a solid globular mass when the zona pellucida is torn. It is, according to Bischoff, solely owing to this firm consistence of the yolk that it, in many cases, preserves its form when a watery fluid passes by imbibition through the zona pellucida, and that an interval is then apparent between the yolk and that membrane.

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[*] Lehrbuch der Physiologie, 2te Ausgabe. Leipzig, 1843, p. 37.

[†] Entwickelungs-geschichte, p. 12; and more recently in his Entwickelungs-gesch. des Hunde-eies, 1845, p. 9.

[‡] Allgemeine Anatomie, p. 965.

[§] Researches on Embryology.

[||] Lond. and Edinb. Phil. Mag. 1835, p. 209.

[¶] Müller's Archiv. 1842, p. 18.

[**] Op. cit. p. 553.

[††] The views of Dr. Barry are explained in the notes at pages 1499 and 1514 of Müller's Physiology.

[‡‡] Op. cit. p. 37.

[§§] Op. cit. p. 14.

[||||] Med. Gazette, vol. xxi. and vol. xxiv.

[¶¶] Allgemeine Anatomie, p. 966.

Owing to the tough consistence of the yolk in the human ovum, Bischoff has not succeeded in isolating its *germinal vesicle;* but he has satisfied himself that it lies near the periphery of the yolk, though not imbedded in a discus proligerus, as it is in the bird's egg.*

The *germinal spot* which lies at that part of the periphery of the germinal vesicle which is nearest to the periphery of the yolk, presents in the mammiferous ovum no appearance of a vesicle or aggregation of cells, but merely that of a finely granulated substance, of a yellowish colour, strongly refracting the rays of light.†

The subjoined table gives the measurements of the mammiferous ovum and its different parts.

	Animal.	Measurements in parts of a Paris inch.	Observer.
Diameter of mature ovum.	Man	$\frac{1}{240}$ to $\frac{1}{120}$	Bischoff.
	Rabbit	$\frac{1}{156}$	Ditto.
	Bitch	$\frac{1}{147}$ to $\frac{1}{142}$	Ditto.
Thickness of zona pellucida	Man	$\frac{1}{2500}$	Ditto.
	Rabbit	$\frac{1}{2500}$ to $\frac{1}{1250}$	Ditto.
	Bitch	$\frac{1}{1666}$ to $\frac{1}{1250}$	Ditto.
Germinal vesicle. . . .	Rabbit Bitch	$\frac{1}{166}$	Ditto.
Germinal spot.	Bitch	$\frac{1}{2500}$	Ditto.
	Mammalia generally	$\frac{1}{3600}$ to $\frac{1}{2400}$	Wagner.
Large yolk globules. . .	Ditto	$\frac{1}{6000}$ to $\frac{1}{4000}$	Henle.

Development of the ovum in the ovary.—The process by which the ovum is formed and brought to its state of maturity is scarcely noticed by Professor Müller. The enquiries of Dr. Barry are not mentioned by him, and those of Valentin only alluded to in a single line. It will be necessary, therefore, to premise here some account of their observations before detailing the results of the more recent researches of Bischoff.

The questions which it seems most important to decide by the aid of the facts revealed by these anatomists are the following:—

1. Is the Graafian follicle the immediate formative organ of the ovum?

2. In what order are the different parts of the ovum formed?

3. What changes do they undergo in the progress of the ovum towards maturity?

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* Op. cit. p. 15.

† Ibid. p. 15 and p. 556.

In the first stages of the development of its internal structure, the ovary, according to Valentin,* closely resembles the testis. A number of streaks are first seen running from the surface of the organ towards the solid axis. These streaks become tubes closed at either extremity, and having membranous walls lined with epithelial globules. In the cavity of these tubes, which are distinctly visible in the embryos of sheep or cows from three to five inches in length, the ovarian follicles are soon developed in the form of cellules, with transparent walls and granular contents, arranged in a linear manner. In proportion as the follicles increase in number and size, the walls of the tubes in which they are contained become thinned, and the central solid axis of the ovary relatively smaller. At length the tubes become so pressed together and displaced by the enlargement of the follicles within them, that the tubular structure is scarcely recognisable. Nevertheless, with some patience the tubes may be distinguished and even demonstrated separately in the young calf, sheep, cat, and rabbit, at the time of birth. While the Graafian follicles enlarge, their contents become more fluid. The fluid part collects in the middle of the follicle, while the granules which from the first have a linear arrangement form an investment, the membrana granulosa, on the inner surface of the follicle. The order in which the different parts of the ovum are developed, Valentin could not ascertain.

These observations of Valentin, though detailed as if they were made with great care, have not been confirmed by either Barry or Bischoff.†

Dr. Barry,‡ it is true, does not appear to have examined the state of the ovary in fœtal animals. It was in young animals, and in those which had just reached puberty that he studied the subject.

The results at which he arrived were that there is a continual disappearance of ova and formation of new ones from a very early age,—that myriads of ovisacs with their contents are formed which never reach maturity, and that the stroma of the ovary always contains innumerable groups of these immature ovisacs. The part first formed, however, according to Dr. Barry, is not the ovisac but the germinal vesicle. This becomes surrounded by a coating of oil-like globules and peculiar granules, and subsequently by a membrane which is the ovisac or Graafian follicle. The ovisac, as yet transparent and structureless, enlarges, and the granules within increase in number. Next a clear space forms around the germinal vesicle, which occupies the centre of the ovisac. In this space the oil-like globules accumulate, and minute opaque granules show themselves amongst them. Thus is formed the yolk, which next becomes separated from the granules in the general cavity of the ovisac by the development of the membrana vitelli, and zona pellucida (now regarded as one membrane). The ovisac, or Graafian vesicle, subsequently acquires an external vascular tunic composed of dense cellular tissue.

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* Müller's Archiv. 1838, p. 526, *et seq.*

† Bischoff expressly states that he has never seen the streaks and tubes described by Valentin, though he sought them in the embryoes of several mammiferous animals, of different ages.

‡ Philosoph. Transact., 1838.

M. Bischoff[*] agrees with Dr. Barry that the development of the Graafian follicles and ova continues uninterruptedly from birth to the end of the fruitful period of woman's life. In some animals, as the cow and sow, it commences in the embryo, even at an early period of uterine existence, but in the dog and rabbit, according to his observation, not till after birth.

M. Bischoff describes the process of formation of the Graafian follicles and ova to be as follows:—At first nothing can be distinguished in the substance of the ovary but primary cells and nuclei of cells. Then round groups of similar cells are seen scattered in large numbers through the stroma. The peripheral cells of each of these groups subsequently coalesce so as to form a homogeneous transparent vesicular membrane, while the portion of the mass within becomes fluid. Thus is formed the Graafian follicle. On the inner wall of this follicle or vesicle new cells are formed in the manner of an epithelial layer, while the cavity is found to contain a transparent fluid with nuclei of cells and granules, exactly resembling yolk granules, suspended in it. The next stage is marked by the appearance of a second smaller transparent vesicle within the Graafian vesicle. This second vesicle, which is the germinal vesicle, has a nucleus, the germinal spot. Granules, similar to yolk granules, soon accumulate around the germinal vesicle; but the further steps in the development of the ovum could not be traced. All its parts were completely formed when M. Bischoff next observed it.

From the preceding account of the observations of Valentin, Barry, and Bischoff, it will be seen that the first and the last of these enquirers agree as to the fact of the ovum being developed within the Graafian vesicle as *its immediate formative organ,* although they differ as to the process by which the Graafian vesicle itself is formed. Bischoff regards the statement of Dr. Barry that the germinal vesicle of the ovum exists before the Graafian follicle as altogether an error.

With regard to the second question proposed at page 35, namely, *in what order are the different parts of the ovum formed?* it appears a matter of certainty that the formation of the germinal vesicle precedes that of the yolk, and the yolk membrane. The observation of Dr. Barry as to this point is entirely confirmed by Bischoff. Whether the germinal spot is formed first, and the germinal vesicle afterwards developed around it, cannot be decided in the case of vertebrate animals. But some recent observations of Kölliker[†] and Bagge[‡] on the development of the ova of intestinal worms show that in these animals the first step in the process is the production of round bodies resembling the germinal spots of ova, the germinal vesicles being subsequently developed around these in the form of transparent membranous cells.

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[*] Entwickelungs-geschichte, p. 365.

[†] Müller's Archiv. 1843, p. 72.

[‡] Diss. de Evolut. Strongyli auricular. et Ascaridis acuminat. Erlangæ, 1841.

The more important *changes that take place in the ovum subsequent to the formation of its essential component parts* consist in alterations of the size and position of those parts with relation to each other, and of the ovum itself with relation to the Graafian follicle, and in the more complete elaboration of the yolk.

The earlier the stage of development the larger is the germinal vesicle in relation to the whole ovum, and the ovum in relation to the Graafian follicle. For, as the ovum becomes mature, although all these parts increase in size, the Graafian follicle enlarges most, and the germinal vesicle least. Changes take place also in the position of the parts. The ovum at first occupies the centre of the Graafian follicle, but subsequently is removed to its periphery. The germinal vesicle, too, which in young ova is in the centre of the yolk is in mature ova found at the periphery.*

The change of position of the ovum from the centre to the periphery of the Graafian follicle is probably connected with the formation of the membrana granulosa which lines the follicle. For, according to Valentin,† at a very early period the contents of the follicle between its wall and the ovum is almost wholly formed of granules, but in the process of growth a clear fluid collects in the centre of the follicle and the granules which from the first have a regular arrangement are pushed outwards, and form the membrana granulosa. Now as the mature ovum lies imbedded in a thickened portion of the membrana granulosa, it seems probable that when the elementary parts of this membrane are pushed outwards in the way just described, the ovum is carried with them from the centre to the periphery of the follicle. While the changes here described take place, the zona pellucida increases in thickness.

With reference to the yolk Valentin ‡ stated that it was richer in granules the younger the ovum. But Bischoff § affirms that the reverse of this is the fact. He says, that in almost all animals the number of the granules of the yolk is greater the more mature the ovum, and that the yolk consequently is more opaque in the mature, and more transparent in the immature ova. The matter in which the granules are contained is, according to Bischoff, fluid in the immature ova of all animals. In some it remains so; but in others, as the human ovum, it subsequently becomes a consistent gelatinous substance.

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* See Bischoff, Barry, Henle, Wagner, Valentin, operibus citatis.

† Müller's Archiv. 1838, p. 533.

‡ Müller's Archiv. p. 534, 1838.

§ Entwick. d. Kaninchen-eies, p. 9; and Entwick. des Hunde-eies, 1845, p. 8.

OF THE SEMEN.*

The few additions which it is necessary to make to the chapter on the subject of the semen, in the Physiology of Professor Müller, may be arranged under the following heads:—

1. Varieties of form presented by the spermatozoids or spermatic filaments.
2. Their structure.
3. Their motion.
4. The influence of reagents upon them.
5. Their modes of development.
6. The question of their independent vitality.
7. Their function.

1. It would serve no good purpose to repeat here the description given by Kölliker † and other recent observers ‡ of the forms of the spermatic filaments in the many species of invertebrate animals, in which they have recently been examined. The general result at which Kölliker arrived, with reference to the forms of the spermatic filaments was, that the varieties of form, though manifold, are comprised within tolerably narrow limits; that the forms are almost always very similar in the same *genus*, and mostly so even in the same *family* and *class;* while in the same *species*, never more than one form is met with.§ The apparent varieties of form observed in certain instances in the same species of animals, are, according to Kölliker's observations, only different stages in the development of one form of spermatic filament.

2. The notion that the spermatic filaments have an internal animal organization, is now abandoned by the best inquirers on the subject. Kölliker || declares that all the hair-shaped filaments, whether spiral or not, are formed of a homogeneous substance. The same is the case, also, he says, in by far the greater number of those that have a body distinct from the filamentous part. With regard to the spermatozoid of the Bear, Kölliker remarks that the circles imagined by Valentin ¶ to be mouth, convoluted intestinal canal, and anus, may have been merely the appearances

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* Book vii. sect. ii. ch. iv. p. 1471, of Müller's Physiology.

† Beiträge zur Kenntniss der Geschlechts-verhältnisse und der Samen-flussigkeit wirbelloser Thiere, Berlin, 1841.

‡ Stein, Müller's Archiv. 1842, p. 238. Von Siebold, Müller's Archiv. 1843, p. 21. Rathke, Wiegmann's Archiv. 1842, i. p. 73. H. Meckel, Müller's Archiv. 1844, p. 473. Will, Horæ Tergestrinæ and Wiegmann's Archiv. 1844, Bd. i. p. 337. Paasch, De Gasterop. nonnull. hermaph. system. genitali et uropöetico. Diss. Berol. 1842. Müller, Ueber den Bau des Pentacorinus caput Medusæ, Berlin, 1843, p. 177.

§ Kölliker, Op. cit.

|| Op. cit. p. 64.

¶ See Müller's Physiology, p. 1473.

presented by the granules of which the spermatozoid was formed.[*] Mr. Gulliver[†] has recently had the opportunity of examining these spermatozoa, and declares that he could detect neither mouth, arms, nor internal vesicles. The dark spot seen in the body of the spermatic filaments of some mammalia, and compared by some writers to a sucker, is believed by Henle,[‡] to be caused merely by a slight concavity similar to that on either side of the human blood-drill. Several observers[§] have noticed that in many of the spermatozoids of the human subject there is, at the junction of the body with the caudal filament, a gelatinous mass or membranous appendage. This appearance, as well as the little prominences on the body and knots on the caudal filament, which are sometimes seen, is probably due to their mode of development, and, at all events, is no evidence of independent animal organization.

3. The rate of the *motion* of the spermatic filaments has been measured by Henle,[||] and found equal to 1 inch in 7½ minutes. The force of the motion was observed by the same physiologist, to be sufficient, easily to displace crystals of calcareous salts, ten times as large as the bodies of the spermatozoids. The body of the spermatozoid presents no movements, no contractions or dilatations.—The caudal filament alone is the seat of motion, and it continues to move when separated from the body. As to the character of the movements, Kölliker insists[¶] that their uniformity distinguishes them from the movements of infucory animalcules, which can vary their movements at will, or in accordance with their perception of external objects. On the other hand, the difference between the movements of the spermatic filaments and cilia, is not greater, he says, than would be expected to result from the one being fixed and the other altogether free.

One phenomenon which must be mentioned here, is the tendency of the spermatozoids to attach themselves to foreign bodies, such as flocculi of fibrin, or epithelium-scales.[**]

4. Wagner has corrected his statement, that strychnine and other narcotics instantaneously arrest the movements of spermatozoids.[††] Solu-

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[*] Appearances due to the same cause probably led Berres to imagine he saw a granular fluctuating mass, a canal filled with coloured matter, and a round vesicle, which might be a stomach or an ovary, in the spermatozoid of the human subject.—Oesterreich. Mediz. Jahrbücher, 1843, p. 141.

[†] Transactions of Zoological Society, February, 1846.

[‡] Allgemeine Anatomie, p. 950.

[§] Dujardin, Henle, Dalrymple, Pouchet, and Wagner. The last-named physiologist thinks the appearance at the root of the tail is the effect of commencing decomposition.

[||] Allgem. Anat. p. 954.

[¶] Op. Cit. p. 66 and p. 80.

[**] Henle, Kölliker.

[††] The same observation has again been made by Prévost, and been advanced by him as an argument in favour of the opinion that the spermatozoids are independent animals. (L'Institut, No. 465.)

tions of these substances produce this effect only when they are so concentrated as to act chemically on the organic substance of the spermatic filaments.

Pure water at first accelerates the movements and then arrests them; at the same time causing the filaments to become twisted on themselves so as to form loops. The latter effect is produced in the most remarkable manner in the hair-shaped filaments of the invertebrata, and in less degree in the pin-shaped filaments of reptiles and Mammalia.*

5. Great additions have been made to our knowledge, of the process by which the spermatic filaments are formed, and the theory of their development has been much simplified. Kölliker, the most successful labourer in this field, proposed in 1841,† the law "that the seminal filaments are developed *either within cells, or by the transformation of cells,* which are formed in the testes at the time of puberty or of heat; the processes of development being analogous to those by which other elementary parts of animals are developed." And he referred the modifications of these modes of development to the following types.

Type I. Each spermatic filament is produced from a single cell by the elongation of the cell itself.

Type II. An entire fasciculus of filaments is produced from each cell, by this first assuming the cylindrical form and then becoming resolved into filaments.

Type III. A fasciculus of many filaments is formed *within* the cavity of a large cell.

Type IV. Each filament is formed *within* a separate cell.

Type V. The filaments are developed in fasciculi from finely granular cells, by the component granules of the cells coalescing in linear series, so as to form fibres, which then increase in length.

Only the third and fourth of these types were observed by Kölliker in the vertebrate classes of animals. The third type was, in fact, the mode of development of spermatozoid discovered by Wagner in birds.‡ The fourth type was discovered by Kölliker in the guinea-pig and mouse. The first stage in the process here observed by him, was the existence of large cells varying from $\frac{1}{166}$ to $\frac{1}{50}$ of a line in diameter. The smaller of these cells contained one or two granulated cellules; the larger cells filled with similar cellules. These granular cellules measured from $\frac{1}{285}$ to $\frac{1}{200}$ of a line in diameter. They were set free by the solution of the large parent cell, and then within each of them a spermatozoid made its appearance, the granules previously contained in the cellule disappearing at the same time. The body of the spermatozoid seemed to be formed by the coalescence of a large number of the granules. The filament was coiled up, and in close contact with the inner surface of wall of the cellule (see figure 3). Wagner* confirmed Kölliker's discovery of this mode of development of spermatozoid, and stated that it prevailed in most, if not all mammalia, and likewise in many birds and reptiles. Henle‡ afterwards conjectured that the third and fourth types of development admitted by Kölliker were essentially identical, that the globules seen by Wagner in the large cells of the semen of singing birds, previous to the appearance of the spermatozoids in those cells were really cellules, in each of which a spermatic filament was developed, and that the only difference between the process in this case, and that discovered by Kölliker in the guinea-pig and mouse was, that in the former the cellules are dissolved, and the filaments set free, the parent cell still remaining entire, whereas in the latter case the parent cell perishes first.

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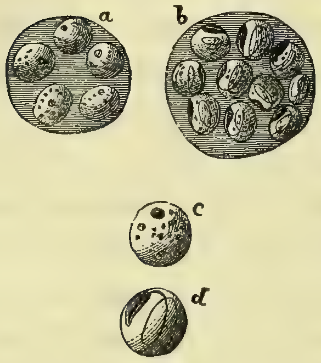
* Wagner's Physiologie.

† Beiträge zur Kenntniss der Geschlechts-verhältnisse und der Samenflüssigkeit wirbel-loser Thiere. Berlin, 1841, p. 53.

‡ See pp. 1475–6 of Müller's Physiology.

Fig. 3.†



This conjecture of Henle has been verified, in some measure, by observations of Dr. Martino, of Naples,§ on the development of spermatozoids in rays and torpedos, but more completely by Kölliker himself, who, in a second memoir,‖ has adduced a large body of evidence in support of the view that the development of the spermatic filaments *within* cells is the universal law. Kölliker believes that in those cases in which (as in the Types I., II., and V. described in his earlier work) spermatic filaments or spermatozoids appear to be formed by the lengthening out and transformation of the cells themselves, the process really consists in the formation of filaments, singly or in fasciculi, *within* the cells, although in many cases the minute size of the cells, and, in some cases, their opacity, render it extremely difficult, or even impossible, to determine the fact absolutely. In all the vertebrate classes, however, except the cyclostomatous fishes, and in many invertebrate animals (insects, arachnoids, cephalopods, and many gasteropods), he has distinctly observed the development of the spermatic filaments within the spermatic cells; and he has further ascertained with certainty in all these animals, insects excepted, that each filament is formed singly within one of the smaller vesicles or cellules, included in the cavity of the parent cell; so that the process is in all essentially the same as that already described as occurring in mammiferous animals. The smaller vesicles, within each of which a filament is formed, and which sometimes exist singly within the larger cells, but more frequently are multiple, were termed by Henle, and formerly by Kölliker himself, cellules, and the enclosing cell was termed the parent cell. But Kölliker now regards the enclosed vesicles as nuclei, each of which has generally, he says, one or two nucleoli. The spermatic filaments, therefore, according to Kölliker, are formed within nuclei.

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* Physiologie, p. 24.

† This figure is taken from Kölliker's more recent memoir, "Die Bildung der Samenfäden." It represents the development of the spermatozoids of the Rabbit. *a.* A parent cell or cyst, with five cellules or nuclei. *b.* A parent cell with ten cellules, each of which contains a spermatic filament. *c.* A free cellule or nucleus, with a nucleolus and granules, more highly magnified. *d.* A cellule in which a spermatic filament is seen, the granules having disappeared.

‡ Allgemeine Anatomie, p. 960.

§ Ann. des Sci. Natur. 1846, p. 297.

‖ Die Bildung der Samen-fäden in Bläschen. Nurenburg, 1846.

The appearance of spermatozoids united in fasciculi, which prevails perhaps in all animals, is not owing to their mode of development, but to their tendency, when set free from their formative cellules or nuclei, to arrange themselves thus; a tendency shewing that their bodies attract each other in the same way that blood-disks do in the formation of *rouleaux.* The fasciculi are formed within the parent cell, when this remains entire after the nuclei or cellules are dissolved; in other cases they are formed in the seminal fluid by the union of spermatozoids which have been wholly set free by the solution of both parent cell and nuclei.

6. The opinion that the spermatozoids are not independent living animals, but merely elementary parts of the organism in which they exist, is becoming generally adopted. Kölliker, Henle, and apparently Wagner, also, as well as Dujardin, take this side of the question.

Besides the arguments adduced by Professor Müller * in support of this opinion, Kölliker urges the narrow limits within which their varieties of form are comprised, a circumstance distinguishing them from Entozoa, and the character of their movements; † but lays especial stress on the fact that they are normal and essential constituents of the seminal fluid. "It cannot be conceived," he says, "that a fluid so important and so strictly vital, in the sense that the blood is vital, which conveys the physical, and even the mental properties of the animal, should be the nidus for the development of foreign and independent beings, whether produced from germs introduced from without, or the result of equivocal generation; and should afford nourishment to these foreign beings while it still retains its own high endowments. And it is still less conceivable that these independent creatures should be the normal, and, indeed, essential parts of such a fluid."

We have already seen that the argument in favour of the spermatozoids being independent animals, drawn from the action of narcotics on them, is not well-founded.

Supposing them to be merely elementary particles of the organism in which they exist, their movements must be ascribed to a cause analogous to those which produce the vibrations of cilia, and the peculiar movements of the sensitive plant.

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* Physiology, p. 1477.

† See *ante* p. 40.

7. Function of the spermatozoids.

That the spermatozoids are normal and essential elements of the semen, is evident from many facts. These facts are the presence of such particles in the seminal fluid of all classes of animals, (the Infusoria being the only class in which they have not been discovered); the large proportion they constitute in the bulk of the seminal fluid, (the fully formed semen consisting almost wholly of a mass of spermatozoids); their close connection with the states of puberty and of heat in the males of all animals (they being first formed at the age of puberty in the human subject, and being periodically produced at each time of heat in animals, while in the intervals they disappear); the presence of these spermatozoids on or about the ova which are observed immediately after fecundation, (Barry, Bischoff, Pouchet, and other recent observers,) and, lastly, the apparently conclusive proof obtained by Prevost,* who filtered frog's semen by means of a bladder, and found that the filtered fluid had not the power of impregnating ova, while the spermatozoids, which did not pass through the filter, still retained the fecundating property.

Bischoff and Valentin, however, think that the fecundating principle itself is contained in the fluid part of the semen, which passes by imbibition through the zona pellucida; and that the function of the spermatozoids is two-fold, first, by their energetic movements to act as carriers of the seminal fluid to its destination at the ovum; and, secondly, by the same active movements, and probably also by some chemical quality, to maintain in its integrity the due mixture and composition of the liquor seminis: acting, in this latter respect, a part somewhat analogous to that performed by the corpuscles of the blood towards the liquor sanguinis.

OF THE DISCHARGE OF OVA FROM THE OVARIES.†

These processes have become the subjects of much discussion during the last few years, and the following questions relating to them have been especially examined.

1. What determines the discharge of ova from the ovary?

2. Is the presence of a corpus luteum in the ovary a sure evidence of previous impregnation?

3. What is the nature and purpose of the function of menstruation?

Respecting the first two questions, the opinions of physiologists have for a long period been extremely various and unsettled. Of late years, however, the opinion has been gaining ground that the discharge of ova from ovary is independent, not only of impregnation, but also of sexual intercourse, and is closely connected with the phenomena of heat in animals, and menstruation in the human female. Bischoff[*] and Raciborski,[†] have at length obtained conclusive evidence of the correctness of this view, as far as it regards mammiferous animals. They have also contributed, with many other contemporary writers, to establish the important fact that *corpora lutea* may be formed under other circumstances than those of impregnation.[‡]

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* L'Institut, 1840, No. 362.

† Book viii. sect. ii. chap. v. p. 1481, of Müller's Physiology.

The following is the law of generation which M. Bischoff lays down as applicable both to Mammalia and to man:—

"The ova formed in the ovaries of the females of the human species and mammiferous animals, undergo a periodical maturation, quite independently of the influence of the male seminal fluid. At these periods, known as those of 'heat' or the 'rut,' in animals, and 'menstruation' in the human female, the ova which have become mature disengage themselves from the ovary and are extruded. Sexual desire manifests itself in the human female with greater intensity at these periods, and in the females of mammiferous animals at no other time. If the union of the sexes takes place, the ovum is fecundated by the direct action of the semen upon it. If no union of the sexes occurs, the ovum is nevertheless extruded from the ovary, and enters the Fallopian tube; but there perishes. The relation in respect of time between the extrusion of the ovum, and its fecundation by the semen, may vary to a certain extent; and the limits of this variation seem to be different in different animals. The seminal fluid may have time to reach the ovary before the ovum is extruded; or the ovum may escape first, and afterwards meet the semen in the Fallopian tube. But the fecundating influence of the semen must be exerted on the ovum before it has quite passed through this tube, otherwise development will not take place; for the development of the ovum commences in the Fallopian tube. It is only at the time of the periodical maturation of the ova that sexual union can have impregnation for its result." *

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[*] Comptes Rendus, 17 Juillet, 1843. Beweis der von der Begattung unabhängiger periodischen Reifung und Loslösung der Eier, Giessen, 1844. Translated by Mr. H. Smith, in Med. Gaz., Jan. 3, 17, &c., 1845

[†] Comptes Rendus, Séance du 17 Julliet, 1843; and De la Puberté et de l'age critique chez la femme et de la Ponte périodique, 8vo. Paris, 1844, p. 405, *et seq.*

[‡] Malpighi, and many other Italian writers after him, asserted that the ova were not only formed, but also discharged from the ovaries, *previous to*, and *independently of*, *fecundation or the union of the sexes;* both their formation and their discharge being effected by the agency of corpora lutea, which these writers regarded as glands produced in the ovaries, even of virgin animals, for that purpose. The ova, when discharged, became impregnated, Malpighi believed, either in the Fallopian tube, or in the uterus. (Malpighi, Opera Omnia, 4to. Lugd. Batav., 1687, p. 222-224).

These views were opposed by Haller, who maintained that the ova of quadrupeds and the human female, are separated from the ovaries, and corpora lutea formed, only in consequence of impregnation; and the weight of Haller's opinion had caused Malpighi's theory, and the facts he announced to be neglected, at all events, in this country, when, in 1817 Sir Everard Home re-produced them as new discoveries. (Lectures on Comparative Anatomy. vol. iv. p. 297. Philos. Transactions, 1817, p. 25, 1819, p. 59.) Sir E. Home gave Malpighi's theory a more complete form, stated the facts on which it was based more precisely, and also connected the discharge of the ova with the phenomena of heat and menstruation, which Malpighi had not done.

Four years later Dr. Power published an Essay on the Nature and Causes of Menstruation, (Essays on the Female Economy, London, 1821,) in which he endeavoured to shew from analogical reasoning and the facts observed by physiologists; 1st. that Menstruation is an effect of the state of orgasm which arises in the ovaries every month; 2nd. that this state of the ovaries is connected with the maturation of the ova, which successively reach maturity after intervals of a lunar month; 3rd. that the mature ovum, if impregnation does not take place, usually perishes within the ovarium, and is removed by the process of absorption; but 4th. that the vascular action in the ovary may, independently of sexual intercourse, be sufficiently great to cause the expulsion of the ovum, and 5th. that in this case a corpus luteum will be formed as a cicatrix of the ruptured Graafian vesicle.

The discovery of the unimpregnated ova in the Graafian follicles of mammiferous animals, by Von Baer, in 1827, afforded a basis for more accurate investigations of the phenomena of impregnation, and of the circumstances under which ova may be discharged from the ovary.

M. Bischoff also maintains, in common with other recent writers, that the discharge of ova at the periods of heat or menstruation, always gives rise to the formation of corpora lutea.

It may be useful to examine the evidence on which these views respecting the maturation and discharge of ova, and the formation of corpora lutea are based.

Ova are matured and discharged from the ovary independently of impregnation and sexual intercourse; and their discharge takes place periodically, namely, at the periods of heat in animals, and menstruation in the human female.

With respect to *mammiferous animals*, lower than man, these statements are undoubtedly correct. In the first place, there is ample evidence to

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Nevertheless, until very recently, but little addition was made to our knowledge on these subjects. The theory of Malpighi, in the modified form which it received from Sir E. Home and Dr. Power, was reasserted with more or less distinctness, by Dr. Lee, in 1834 (Cyclopedia of Practical Medicine, Art. Ovary.), M. Gendrin, in 1839 (Traité Philosophique de Médecine Pratique, tom. i. p. 28, *et seq.*), Dr. W. Jones, in 1839 (Practical Observations on Diseases of Women, London, p. 157, *et seq.*). M. Negrier, in 1840 (Recherches Anatom. et Physiol. sur les Ovaries, Paris), Dr. Paterson, in 1840 (Edinburgh Med. and Surg. Journal, vol. 53, p. 62), Mr. Girdwood (Lancet, 1842-1843, vol. i. p. 825), and M. Pouchet, in 1842 (Théorie Positive de la Fécondation, Paris).

But although facts of great interest had been adduced by many of these authors, in support of their theory, and had been detailed by them with more accuracy than by the earlier writers, yet these facts were not in their nature new, and were not generally received as conclusive proofs. M. Bischoff and M. Raciborski were the first to apply the light afforded by Baer's discovery to the elucidation of this subject, and to demonstrate the unimpregnated ovum of a mammiferous animal in the Fallopian tube, after its escape from the Graafian follicle. The observations of M. Bischoff and those of M. Raciborski, were published at the same time, but the descriptions given by the former are much the more detailed and precise.

* Beweis, &c., p. 4.

prove that in these animals, as in the lower classes, ova are discharged from the ovaries independently of the influence of the male.

Several experimenters Dr, Blundell,[*] Hausmann,[†] and Bischoff,[‡] have observed that, when one oviduct, or one half of the uterus has been tied or divided in an animal previous to coitus, although fœtuses are subsequently met with only on that side on which the passage to and from the ovary remains free, yet ruptured ovarian vesicles, or corpora lutea, are found in *both* ovaries. And Dr. Blundell has shewn that the result, as regards the ovaries, is the same, if the vagina be divided near to the mouth of the uterus, so as completely to interrupt its canals, and to prevent the seminal fluid from reaching even the uterus, although, of course, no embryos are produced in this case. These experiments proved that Graafian follicles burst independently of the contact of the seminal fluid; but still they left room for the objection that the rupture of the follicles might have been caused by the excitement attending sexual connection. This objection, however, does not apply to the fact vouched for by many writers of high authority—Cruikshank, Sir E. Home,[§] Paterson,[||] Hausmann,[¶] Raciborski,[**] and Bischoff,—and now almost universally admitted, that if mammiferous, which have been kept separate from the male, be killed during the period of heat, the Graafian follicles will be found either turgid and extremely vascular, or already burst and in various stages of conversion into corpora lutea.

All the foregoing observations were, however, defective inasmuch as they did not demonstrate the ova which had escaped from the ovaries. This deficient link in the chain of evidence has been supplied by M. Bischoff and M. Raciborski. The following is an abridged account of one of M. Bischoff's important observations.[††] On the 18th and 19th of December, 1843, he remarked that a large bitch in his possession commenced to be in heat. He kept her closely shut up, and on the 23rd (having previously, on the 21st, ascertained that she was disposed to receive the male, though he did not permit coitus to take place) he cut out the left ovary and Fallopian tube, and closed the wound by suture. On examining the ovary he found that no Graafian follicles had yet opened, though four of them were much swollen, undergoing the changes preparatory to the discharge of the ova. Five days later he killed the animal and he now found that rupture of the follicles in the remaining right ovary had taken place. Four corpora lutea were well developed.

Bischoff now sought for the ova. Having carefully dissected the

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[*] Medico-Chirurgical Transactions, vol. x. p. 254. Experiments on Rabbits.

[†] Ueber die Zeugung des wahren Weiblichen Eies. Hannover, 1840, p. 93.

[‡] Beweis, p. 10-17.

[§] Philos. Transact. 1817, 1819.

[||] Ed. Med. and Surg. Journal, vol. liii. p. 64.

[¶] Ueber die Zeugung des wahren Weiblichen Eies. p. 94, 95, and 96.

[**] Op. Citat. p. 376, *et seq.*

[††] Beweis, p. 28.

Fallopian tube, extended it upon a wax tablet, and opened it with a pair of fine scissors, he found the four extruded ova, far advanced in the cavity of the tube; they were close together, at a distance of three inches (Paris measure) from the ostium abdominale. Three of these ova had the usual round form; the fourth had an anomalous shape. All had still the discus around the zona; but it was clear that the cells of the discus no longer retained their full normal appearance, but had already begun to undergo liquefaction. Similar observations were made by Bischoff on a sow and a rat. M. Raciborski also found an ovum in the oviduct of a bitch that had been kept, during the period of heat, separate from the male.

It is certain, then, that in mammiferous animals, as in the lower classes, ova are brought to maturity and discharged from the ovaries independently not only of the direct action of the semen, but also of the excitement attending sexual union. The following facts and considerations seem to render it almost as certain that this phenomenon of the maturation and extrusion of the ova takes place periodically; namely, at those times which are marked by the phenomena of heat or rut. Before the age of puberty, when the first period of heat occurs, no corpora lutea are to be found in the ovaries; but at this time they make their appearance, even though the animal should be kept separate from the male.* Then it is to be remarked, that in all the instances recorded with any degree of minuteness of Graafian follicles presenting the appearance of being recently ruptured, the animals were at the time, or had recently been, in heat; and that, on the other hand, there is no authentic and detailed account of Graafian follicles being found ruptured in the intervals of the periods of heat. Again, the fact that female animals do not admit the males, and never become impregnated, except at those periods, strongly confirms the idea that ova are discharged at no other times.

That the maturation and discharge of ova takes place normally at *every period* of heat, although it cannot be said to be proved, is at least in the highest degree probable. The instances in which the Graafian follicles have been found ruptured in animals in heat are already numerous; and it is generally admitted, even by authors who deny the bursting of the Graafian follicles, or at least the formation of true corpora lutea except as consequences of impregnation, that at every period of heat in animals the ovaries become turgid with blood, and that a certain number of vesicles at the same time enlarge and become very vascular.†

It has been shown, too, by Dr. Barry,‡ as well as by Bischoff in his earlier researches, that the ova in those vesicles which are enlarged at the periods of heat, themselves present certain changes in their size and structure which may be regarded as signs of their maturity. And experiments, such as the one on the bitch just quoted from Bischoff, seem to show that the turgid state of the Graafian follicles is preparatory to their spontaneous rupture and the discharge of the matured ova.

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* Sir E. Home, Phil. Transactions, 1819.

† Cruikshank, Phil. Trans. 1797. Hausmann, Op. Cit. p. 73. Paterson, Edin. Med. & Surg. Journal, vol. liv. pp. 394 and 401.

‡ Phil. Trans. 1832, Part ii. p. 310, par. 125.

It is almost impossible to doubt, therefore, that in mammiferous animals every period of heat is normally accompanied, not merely by a vascular turgescence of the ovaries and their Graafian follicles, but also by the maturation of a certain number of ova, and their extrusion from the follicles which contained them; and that all this takes place independently of sexual intercourse.

We have now to inquire whether the *human* female is subject, in this respect, to the same law as the female of other mammiferous animals; whether ova are discharged from the human ovary under any other circumstances than those of impregnation; and, supposing this first question to be answered in the affirmative, whether the maturation and discharge of ova occurs periodically at the epochs of menstruation.

Respecting the former of these questions scarcely any doubt can be entertained. Ovarian follicles recently ruptured have been seen so frequently, and by so many independent observers,* in the ovaries of virgins or women who could not have been recently impregnated, that it must be regarded as certain that the follicles of the human ovary do burst from other causes than impregnation or sexual connexion; and although it is true that the ova discharged under these circumstances have not hitherto been discovered in the Fallopian tube, yet analogy forbids us to doubt that in the human female, as in the domestic quadrupeds, the result and purpose of the rupture of the follicles is the discharge of the ova. Whether the maturation of ova and the discharge of them from the ruptured follicles in the human female takes place periodically at the epochs of menstruation, cannot, at present, perhaps, be decided with absolute certainty; but the evidence in favour of the affirmative of the question greatly preponderates.

In the first place, it is agreed by all authors who have touched on the point, except Dr. Ritchie, that no traces of follicles having burst are ever seen in the ovaries before puberty or the first menstruation. Secondly, all the writers who have described the particulars of the cases in which the ovarian follicles were found burst independently of sexual intercourse, with the exception again of Dr. Ritchie, state that the women were at the time menstruating, or had very recently passed through the menstrual state.

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* Sir E. Home, Phil. Trans. 1817. Dr. Blundell, Physiol. and Pathol. Researches, 1824, p. 56, Med. Chir. Trans. 1819, p. 268. Dr. Lee, Cyclopedia of Medicine, Art. Ovary. 1834; Lectures on Theory and Practice of Midwifery, 1844. Gendrin, Méd. Pratique, t. i. p. 28. W. Jones, Practical Observations on Diseases of Women, 1839, p. 157. Paterson, Edin. Med. and Surg. Journal, vol. liii. Laycock, Medical Gazette, 1840. Devaix, Gazette Médicale. Raciborski, Bischoff. Girdwood, Dr. Ritchie, Pouchet, loc. citat. M. Serres, Comptes Rendus, Nov. 18, 1844.

Thirdly, although in women, sexual connexion is not confined to these periods, yet it is an old observation, confirmed by the experience of some eminent modern accoucheurs, and by the results of inquiries instituted by M. Raciborski, that conception is more likely to occur within a few days after the cessation of the menstrual flux than at other times: and hence the distinguished obstetrician, Naegeli, is accustomed to reckon the duration of pregnancy at nine months and eight days from the last menstrual period, and in normal cases has, he says, never been wrong. These are strong grounds for believing that the discharge of ova is confined to the periods of menstruation.

The number of facts at present collected are insufficient to establish it as a law that an ovum is discharged from the ovary of the human female *at every normally developed period of menstruation.* Yet it must be observed that although the diseases causing death must, in the majority of instances, disturb the function of the ovaries, and prevent the extrusion of the ovum, yet to each of those inquirers who have been on the watch for such cases, several instances of ruptured follicles in menstruating woman have occurred within a short space of time. And the fact that the ovaries of the human female become turgid and vascular at the menstrual periods, as those of animals do at the time of heat, strongly favours the opinion that the generative system of the human female is subject to the almost universal law of the periodical discharge of ova.*

The discharge of an ovum always gives rise to the formation of a corpus luteum.

This is the statement of M. Bischoff. But most of the recent writers on the subject, Paterson, Lee, Ritchie, Raciborski, Deschamps, and Renaud maintain, at all events as regards the human female, that a true and fully formed corpus luteum is met with only where an ovum has been impregnated; and, consequently, that such a body is a sure evidence of previous impregnation. Most of these writers lay great stress on the distinction to be drawn between true and false corpora lutea.

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* Dr. Ritchie, however, adduces some observations, which, if confirmed, would shew that the operation of this law is much modified in the human subject. He states that ovarian follicles are found ruptured even before the commencement of menstruation, as well as during its subsequent suspension, whether this arises from normal causes or a disordered state of the system. He admits, however, that the full development of the ova and the Graafian follicles is generally, though not necessarily, associated with menstruation, (Contributions, second series, part ix. Med. Gaz. vol. xxxvi. p. 811,) and that only those of follicles which burst at or about the time of menstruation, undergo further organic development, or changes in their coats. (p. 982.) The openings, too, in the peritoneum over the ovarian follicles of the amenorrhagic or non-menstruating female, Dr. Ritchie states, are punctiform, while in the menstruating female they are uniformly linear or crucial and of much larger size. This difference he ascribes to the greater activity of the ovaries in menstruating, than in other women. (p. 325.) Dr. Ritchie also maintains that menstruation may occur several successive times without the evolution of an ovum; founding this statement on his examination of the ovaries of women who had menstruated regularly. (p. 940.) But this, it is obvious, is no formidable objection to the theory that the extrusion of ova is connected with the function of menstruation. For the organic excitement and vascular turgescence of the ovaries, on which menstruation certainly depends, may have been sufficient to determine the occurrence of the latter function, but yet, from some cause or other, inadequate to produce the rupture of an ovarian follicle. In some cases, too, it may, and in all probability, does happen, that ova are matured, and the follicles prepared for bursting, yet the discharge of the ova is prevented by a thickened state of the peritoneal covering of the ovary.

In order the better to judge of the value and correctness of their views it will be well in the first place to inquire what is the structure and mode of growth of a corpus luteum formed during pregnancy in mammiferous animals as well as in man.

The corpus luteum of mammiferous animals when fully formed is a roundish solid body, of a yellow or orange colour, and composed of a number of lobules which surround, sometimes a small cavity, but more frequently a small stelliform mass of white substance; the delicate processes given off by this white mass passing as septa between the different lobules of the yellow body. Very often in the cow and sheep, there is no white substance in the centre of the corpus luteum; and the lobules projecting from the opposite walls of the Graafian follicle, appear in a section to be separated by the thinnest possible lamina of semi-transparent tissue.

It is an important fact, that the development of the *corpus luteum* commences before the rupture of the Graafian follicle. The follicle which is about to burst and expel the ovum, becomes highly vascular and also opaque; and *immediately* * before the rupture takes place, its walls appear thickened on their interior by a reddish, glutinous or fleshy substance. Immediately after the rupture the inner layer of the wall of the follicle appears pulpy and flocculent. It is thrown into wrinkles by the contraction of the outer layer, and soon red fleshy mammillary processes grow from it, and gradually enlarge till they nearly fill the follicle, and even protrude from the orifice in the external covering of the ovary. Subsequently this orifice closes, but the fleshy growth within still increases during the earlier period of pregnancy, the colour of the substance gradually changing from red to yellow, and its consistence becoming firmer.

The corpus luteum of the human female differs from that of the domestic quadruped, in being of a firmer texture and having more frequently a persistent cavity at its centre, and in the stelliform cicatrix which remains in the cases where the cavity is obliterated, being proportionally of much larger bulk.

The following are the more obvious phenomena of its formation:—First, the Graafian follicle which is about to discharge its contents, becomes very vascular, then its walls lose their transparency and a very thin layer of soft yellowish matter appears in them.* When the follicle bursts, this yellowish deposit increases. It does not, however, usually form mammillary growths projecting into the cavity of the follicle, and never protrudes from the orifice, as is the case in other mammalia. It maintains the character of a uniform, or nearly uniform layer, which is thrown into wrinkles in consequence of the contraction of the external tunic of the follicle. After the orifice of the follicle has closed, the growth of the yellow substance continues during the first half of pregnancy, till the cavity is reduced to a comparatively small size, or is obliterated; in the latter case, merely a white stelliform cicatrix remaining in the centre of the yellow body.

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* The time, according to Bischoff's observation, (Entwickelungs-geschichte, p. 32,) must be very short.

In some mammalia as well as in the human subject, an effusion of blood generally takes place into the cavity of the Graafian follicle at the time of its rupture, but in the latter it is more constant and in greater quantity than in the former. The effused blood, however, has in no case any share in forming the yellow body. It gradually loses its colouring matter and acquires the character of a mass of fibrin. The serum of the blood sometimes remains included within a cavity in the centre of the coagulum, and then the decolorized fibrin forms a membraniform sac, lining the corpus luteum. At other times the serum of the blood is removed, and the fibrin constitutes a solid stelliform mass.

There has been much difference of opinion as to the origin of the growth which forms the yellow body. But most of the modern writers of high authority who appear to have examined the corpora lutea in the earliest stage of their growth, with the aid of the microscope, Valentin, R. Wagner, Bischoff, Raciborski, and Zwicky, corroborate the statements of Haller and Von Baer, that the growth arises from the inner surface of the follicle; and shew that it is, in fact, the result of an increased development of the cells forming the membrana granulosa which lines the internal tunic of the Graafian follicle.

The mode of formation of the corpus luteum in the cow and sow has been made the subject of a minute microscopic investigation by Zwicky, the accuracy of which, in all important points, has been verified by the writer.

The Graafian follicle, according to Zwicky, has really but one tunic or theca, which, although separable into two layers, is throughout composed of the same elements; namely, granular nucleated cells, in part round and varying in size, and in part becoming elongated into fibres (fibro-cells). (Fig. 4, A.) The conversion of the cells into fibres is further advanced in proportion as they are nearer to the outer surface of the theca, where they can no longer be distinguished from the fibres forming the stroma of the ovary. Floating in the fluid contents of the follicle, are granular nucleated cells, round, ovate, or fusiform, and similar to those forming the innermost stratum of the theca.

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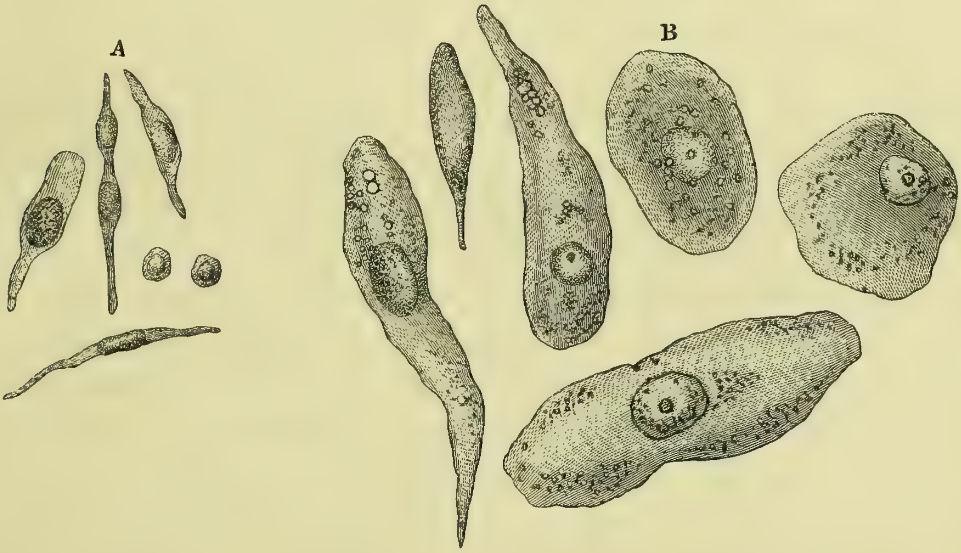
* Negrier, Ritchie.

When the follicle enlarges at the time of heat, and before the escape of the ovum, the cells floating in the fluid, and those forming the inner surface of the theca, undergo a twofold transformation. Some merely become elongated and present the various stages of transition into fibres, while others become much enlarged in all directions, acquiring four or five or even ten times their original diameter; their nuclei at the same time attaining double their former size, and presenting very distinct nucleoli.

These enlarged cells are marked with granules of fatty matter of yellow colour (fig. 4, B), some of these granules are contained within the cells, but others are adherent, M. Zwicky thinks, to their outer surface while the greater part lie free in the interstices of the cells. When the large cells have attained their full size they either burst or become elongated, so as to form fibres which are distinguished from the fibres resulting from the direct transformation of the smaller cells, by their breadth, the large size of their nuclei, and the presence of fat granules in them. Cells presenting all these varieties of form may be found in the fully formed Graafian follicle immediately previous to the escape of the ovum; some floating in the fluid contents, others forming plicæ or villi on the inner surface of the theca.*

Fig. 4.



In a follicle from which the ovum has recently escaped, the theca is thicker, and its inner strata are of a loose texture and red colour, and consist chiefly of the large cells above described, mixed with some small nucleated cells in part elongated into fibres, a few bodies resembling the nuclei of the large cells, and numerous free, yellow, or orange coloured fat granules. The external strata of the theca present no change from their early condition.

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* It may be doubted whether these large cells are not altogether new formations. M. Zwicky gives no very satisfactory evidence of their being even in part developed from the small cells of the immature Graafian follicle.

The further progress in the formation of the corpus luteum consists in the continued growth, or as it were vegetation, of the internal strata of the theca towards the cavity of the follicle; this growth of the theca being dependent on the continued increase in size of its component cells, and the development of new cells of the same kind.

In the fully formed corpus luteum the nucleated fibres resulting immediately from the transformation of the smaller cells are disposed in fasciculi which traverse the mass, and form, as it were, a frame-work, apparently destined to support the nutrient vessels. The large cells and fibro-cells distinguished by the fat granules they contain, seem to have no regular arrangement.*

Respecting the mode of development of the human corpus luteum very various opinions have been held; some writers, as Dr. Montgomery, Dr. Paterson, Dr. Ritchie, and Dr. Frank Renaud,† maintaining that the yellow substance is deposited between the two tunics of the Graafian follicle; others, as Dr. Lee, asserting that the growth of the yellow substance takes place external to both tunics: while most of the German and French writers assume, and M. Raciborski ‡ states, from direct observation, that as in the mammalia, so in the human subject, it is the inner surface of the tunic that produces the yellow body. That the last view is the correct one the writer is satisfied, from the results of the examination of many human corpora lutea in various stages of their growth. For in several which were in an early stage, no membrane whatever could be demonstrated on the interior of the layer of yellow substance, and a particle taken from its inner surface was found on microscopic examination to consist of the elements already described as forming the corpora lutea in domestic quadrupeds. Where a membrane did exist on the interior of the yellow substance it was found to be composed of elements very different from those which constitute the inner strata of the tunic of the Graafian follicle,—it was composed not of granular nucleated cells, nor of fibro-cells, but of the delicate non-nucleated fibres into which the fibrin of the blood or liquor sanguinis is transformed subsequent to its coagulation.

The microscopic elements of the fully formed corpora lutea are essentially the same in the human subject as in the domestic animals.§

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* The corpus luteum of the sow and cow, is, according to Zwicky, never entirely re-absorbed. But, by the rupture of some of the larger cells, the transformation of others into fibro-cells, and the subsequent absorption of the greater part of these fibro-cells, it is at length reduced to a small mass, consisting of imperfectly-formed fibres of cellular tissue, mixed with dark yellow fat, the quantity of which is proportionally much greater in corpora lutea which are undergoing diminution in size, than in those which are still at the maximum of their development.

† Cormack's Monthly Journal of Medical Science, vol. v. 1845, p. 600.

‡ Bulletin de l'Acad. Roy. de Médecine, 15 Oct. 1844.

§ This statement is founded on the writer's own observations, as well as on the descriptions of Raciborski and Renaud.

Having thus learned the structure and mode of formation of the corpora lutea which are seen in impregnated animals we have now to enquire whether such bodies are always produced as a consequence of the rupture of Graafian follicles, and the discharge of their ova. This question must undoubtedly, with some limitation, be answered in the affirmative, as far as it regards quadrupeds in the state of heat. For even if the statements of the older anatomists, who speak of having found corpora lutea in unimpregnated animals, were left out of consideration, the more recent observations of Sir E. Home, Dr. Blundell, M. Raciborski, and M. Bischoff, would render it certain that the extrusion of ova from the Graafian follicles of animals in heat, is attended with the formation of corpora lutea even when the extruded ova do not become impregnated. In the figures, given by Sir E. Home * and M. Bischoff,† of corpora lutea formed under these circumstances, it is evident that the growth of the yellow substance has proceeded to such an extent as to protrude from the orifices of the ruptured follicles, after filling their cavities. These are certainly corpora lutea which could not be distinguished from corresponding bodies of the same stage of development in the ovaries of impregnated animals. In the impregnated animal, however, the corpus luteum continues to increase in size after the orifice in the follicle has closed; and whether this is the case in animals which are not impregnated is doubtful. It is probable that if the ova have not been fecundated, the state of orgasm of the ovaries and Graafian follicles, which arose during the condition of heat, subsides, and that the corpora lutea then, instead of continuing to grow, quickly shrivel and disappear. For if it were not so, if the corpora lutea attained their full size in unimpregnated animals, the ovaries of those animals in which the period of heat recurs after short intervals, would constantly be found to contain fully formed corpora lutea; and this is not the case.

With regard to the human female the limitations with which the rule may be admitted are greater. There is reason to believe that under normal circumstances the rupture of a Graafian follicle and the discharge of an ovum at the period of menstruation is attended with that change in the tunic of the follicle which constitutes the first step in the formation of the corpus luteum. For amongst the descriptions given by writers ‡ of ruptured Graafian follicles found in virgins and other menstruating women who could not have been recently impregnated, there are several in which it is distinctly stated that a layer of yellow substance existed in the walls of the follicle; and in other instances, bodies resembling in structure the corpora lutea of pregnant women have been found in the ovaries of females who had menstruated at some distance of time, and who had not been pregnant.§

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* Lectures on Comparative Anatomy, vol. iv.

† Ann. des Sc. Nat., 1844.

‡ Dr. Lee, Dr. Paterson, Dr. Ritchie, Renaud, op. citatis.

§ Dr. Ritchie's case. x. part i. sec. ii. Medical Gazette, and Dr. Blundell's case, seem to have been unquestionably of this nature.

But the layer of yellow matter in the recently ruptured follicle was in such cases very thin, and the yellow body though in all other respects similar to the corpus luteum of a pregnant woman, was of much smaller size. It appears, therefore, that the development of the corpus luteum does not proceed so far in the menstruating woman as in animals in heat. The reason of this inferior degree of development of the corpus luteum in the woman, in comparison with that in quadrupeds, is easily conceivable; the excitement of the ovaries and the whole sexual system being undoubtedly far greater in the female quadruped in the state referred to than it usually is in the human female at the period of menstruation.* The degree of vascular excitement in the generative organs attending the process of menstruation is moreover liable to great variety. It may sometimes be only just sufficient to cause the rupture of the follicle, and not adequate to the production of yellow substance by an organic change in its tunic. In this way we may account for the fact that in the greater number of the descriptions of ruptured Graafian follicles observed in unimpregnated women, no mention is made of the existence of a yellow deposit in the walls of the follicle. The follicles thus destitute of yellow substance when collapsed would form the *corpora albida* of Dr. Ritchie. On the other hand we must admit that when great excitement attends menstruation the formation of the corpus luteum may go on more rapidly and continue for a longer period, and that under these circumstances the resulting yellow body may be of considerable size.

If, in addition to the foregoing facts and considerations, the varieties in size of the corpora lutea formed during pregnancy are borne in mind, it will be seen that cases can seldom occur where the mere presence of one of those bodies can be taken as a proof of previous impregnation. The following practical rules, however, seem to be deducible from the facts detailed.

1. A corpus luteum, in its earliest stage (that is a large vesicle filled with coagulated blood, having a ruptured orifice, and a thin layer of yellow matter in its walls), affords no proof of impregnation having taken place.

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* The fact is announced by M. Raciborski, (Acad. de Médecine, Séance du 15 Oct. 1844. Gaz. Med. Oct. 19, 1844,) as a deduction from his experiments and dissections, in the following terms: "In the females of most of our domestic animals, whether they have or have not had sexual intercourse with the males, the expulsion of the ovule is always followed by the formation of a corpus luteum, a fleshy mass, of a yellow or reddish colour. It is different, however, with women. If the expulsion of the ovule, at the period of menstruation, is not followed by conception, the granulations on the inner surface of the Graafian follicle increase in size; but this activity of nutrition soon ceases after it has produced a thin membrane, of a yellow colour, lining the proper membrane of the follicle, and enclosing a cavity in which traces of a clot of blood may be found. If, on the contrary, conception should take place, the elements of the granular layer of the follicle continue to increase in number and volume, until, in a short time, they form a mass of sufficient volume to fill the whole cavity of the follicle."

2. From the presence of a corpus luteum, the opening of which is closed, and the cavity reduced or obliterated, only a stellate cicatrix remaining, also no conclusion as to pregnancy having existed or fecundation having occurred can be drawn, if the corpus luteum be of small size, not containing as much yellow substance as would form a mass the size of a small pea.

3. A similar corpus luteum of larger size than a common pea, would be strong presumptive evidence, not only of impregnation having taken place, but of pregnancy having existed during several weeks at least; and the evidence would approximate more and more to complete proof in proportion as the size of the corpus luteum was greater.

What is the nature and purpose of the function of menstruation?— This question has reference chiefly to the theoretical views deduced from the facts detailed in the preceding pages. Bischoff, and the other physiologists, who believe that ova are normally expelled from the ovary at the periods of heat in animals, and of menstruation in the human female, regard those two states, heat and menstruation, as perfectly analogous. The essential character of both, according to their view, is the maturation and extrusion of ova. In both there is a state of active congestion of the sexual organs, sympathizing with the ovaries at the time of the highest degree of development of the Graafian follicles; and menstruation is only the crisis of this state of congestion.*

This theory is principally based, first on the long admitted fact that the changes which take place in the female system at the time of puberty, and the periodic recurrence of menstruation from that epoch to the end of the fruitful period of woman's life, are dependent on the presence and healthy condition of the ovaries; secondly, on the fact, which has also long been known, that at every period of menstruation, as at every period of heat in female animals, a vascular turgescence of the ovaries takes place; and thirdly, on the more recently alleged fact, that at the period of menstruation in women, as well as at the time of heat in animals, ova are normally extruded from the ovaries.

The two main arguments used by those physiologists who have denied the existence of an analogy between heat and menstruation, are that the heat is characterized by an excited state of sexual desire in the female, and by the occurrence of coitus at that time exclusively, while the menstruating woman has no strong feeling of sexual desire, and is repulsive to the male sex; and that a true menstrual discharge of bloody fluid is not observed in animals.

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* Raciborski, Op. Cit. p. 446. See also Dr. Lee's remarks in Cyclop. of Med. Art. Ovary; and M. Pouchet's, in his work, Théorie Positive de la Fécondation, p. 87, *et seq.*; and more recently in an enlarged edition of this work under the title of Théorie Positive de l'Ovulation Spontanée et de la Fécondation des Mammif. et de l'espèce humaine. Paris, Baillière, 1847, p. 227, *et seq.*

In answer to the first of these arguments, Bischoff says, that "no such essential difference between the conditions of heat and menstruation exists. The female quadruped at the commencement of the state of heat appears to be in a state of general suffering, and will not admit the caresses of the male; it does not seek the coitus until this first stage of the heat is passed. The human female, on the other hand, at the time of the cessation of menstruation feels herself unusually well, and is more than ordinarily disposed for sexual connection. So that there is in this respect a most complete accordance between the two functions." * M. Bischoff might have added, that the less marked development of the sexual feeling in woman at the periods of menstruation, than in female quadrupeds at the periods of heat, corresponds with a fundamental mark of distinction between man and the brute. In animals it is natural that the instinct inducing the act of coitus, should be strongly developed at the times when that act may have for its result the fecundation of ova, and that the instinct should not exist at other times when no ova are prepared for fecundation. In women such a strong development of the sexual feeling, and aptitude for sexual intercourse, exclusively at particular times, would have been in contradiction to the freedom of will and self-command which characterizes the human species.

With regard to the argument founded on the hemorrhagic nature of the menstrual discharge in women, Raciborski † remarks that this discharge is not the essential phenomenon of menstruation—that women have become pregnant who had never menstruated; that although the discharge attending the heat in quadrupeds is in most cases simply mucous, yet in many of them it is occasionally bloody, and in some, nearest to man, consists chiefly of blood; ‡ and, on the other hand, that although the menstrual discharge in women is essentially bloody, yet at the commencement and end of menstruation, the blood is mixed with an increased flow of mucus, and with epithelium thrown off from the mucous surfaces of the sexual passages.

Assuming, now, that the theory of the discharge of ova periodically at the times of menstruation, and exclusively at those times, is correct, as it certainly is highly probable, the question next presents itself,—how long after the extrusion of the ovum from the ovary, or how long after the cessation of the menstrual discharge is fecundation possible. The passage of the ovum from the ovary to the uterus occupies, M. Bischoff says, three days in the rabbit, and four or five days in ruminants, and, therefore, probably eight or ten days in the human female. M. Bischoff believes that the ovum escapes from the Graafian follicle at the time when the menstrual discharge is about to cease, and he is of opinion, that in order to be fecundated, it must be acted on by the semen while it is in the Fallopian tube. From these data, then, he infers that sexual connection,

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* Beweis, p. 40.

† Op. Citat. p. 444, *et seq.*

‡ See also Girdwood, Lancet, Dec. 1844, for facts of this nature.

to be fruitful, must take place within eight or twelve days from the cessation of the menstrual discharge.* Raciborski † thinks the time more limited. Out of sixteen women who gave him such information as enabled him to determine the time of fecundation, there was only one in whom this occurred so late as ten days after the cessation of the menstrual flux; and in this one the menses had been suddenly arrested several days before their usual time of cessation, so that the extrusion of the ovum, M. Raciborski thinks, did not take place till about two days prior to the act of sexual intercourse, to which it owed its fecundation. M. Raciborski relates several cases which seem to shew that impregnation may result from sexual coitus taking place one or two days before the period of menstruation. In one of these cases the menses did not appear at all; in three others they continued an unusually short time.

OF FECUNDATION.‡

UNTIL very recently, the opinion prevailed that in every case of impregnation, the seminal secretion made its way from the uterus along the Fallopian tubes to the ovary, where its fecundating influence was exerted on the ovum or ova, which were sufficiently mature to be acted upon; and by many it was also supposed, that unless the seminal fluid reached the ovary, no ova were extruded. Hence the statement of Professor Müller,§ that in Mammalia, impregnation is always effected at the ovary. Hence also the early remark of Bischoff, that in rabbits a period of from nine to ten hours, in bitches of from twenty to twenty-four hours, after the union of the sexes, elapses before any ova are extruded from the ovary. More recent experiments, made especially by Bischoff || himself, have proved, however, as already related, that the maturation and escape of ova from the ovary, is an event totally independent of the arrival of seminal fluid at the latter organ, and independent even of any union of the sexes. It is true that, as shewn especially by the experiments of Bischoff, sexual union in rabbits, bitches, and probably most other Mammalia, usually takes place previous to the extrusion of ova from the ovary (though this is denied by M. Pouchet ¶), and that sufficient time often elapses for the seminal fluid to reach the ovary before such extrusion occurs. And, doubtless, in these latter cases, fecundation of the ovum or ova is effected at the ovary itself. But the fact of ova having in several instances been

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* Beweis, p. 44. More recently (Müller's Archiv. 1844. Jahresbericht, p. 132) Bischoff states as his conclusion from analogical reasoning and facts communicated to him, that the time of fruitfulness is limited to the twelve or fourteen days succeeding each menstrual period.

† Op. cit. p. 457, *et seq.*

‡ Müller's Physiology, p. 1488.

§ Physiology, p. 1491.

|| Beweis, &c. and Entwickelungs-geschichte des Hunde-eies.

¶ Theorie Positive de l'Evol. Spontan. &c. 1847, p. 372.

found considerably advanced along the Fallopian tube in animals killed immediately after or even before sexual union, not only proves the spontaneous maturation and discharge of ova from the ovary, but also renders highly probable the opinion, that not merely at the ovary, but at any part of the tract from this organ to the uterus at which the ovum first comes in contact with the seminal fluid, fecundation of it may be there effected. Bischoff[*] is of opinion that the ovum may sometimes be fecundated at the ovary, but that most commonly it escapes from this organ previous to the arrival at it of the seminal fluid, and that fecundation is then effected in the Fallopian tube. He considers that by the time the ovum reaches the uterus, or even the lower end of the Fallopian tube, its capacity for being impregnated is lost. His reasons for this supposition, are founded on the changes indicative of impregnation observed in the yolk of the ovum previous to its entrance into the uterus, and on the complete cessation of the sexual desire in those animals in which, after death, he found that the ova had passed into the uterus, or had arrived at the lower part of the Fallopian tube. Pouchet,[†] on the other hand, maintains that it is *only* in the uterus or the lowest part of the Fallopian tube, that fecundation takes place, for, according to his statement, the seminal fluid never penetrates so far as the ovary, and seldom, if ever, extends beyond the middle of the Fallopian tube. He believes that Bischoff and Wagner must have mistaken for spermatozoids on the ovary a form of Entozoa, which he describes under the name of Pseudo-zoospermes.[‡]

No confirmation has been afforded to the opinion entertained by Prevost, and Dumas, and by Dr. Barry,[§] that the spermatozoids enter bodily into the ovum, and as believed by the first-named observers, constitute the embryo. Neither has any other embryologist succeeded in finding any opening or fissure in the zona pellucida, through which the spermatozoids might be enabled to enter the ovum, as was described by Dr. Barry:[||] Bischoff, who has repeatedly but fruitlessly made search for such an opening in the ova of bitches and rabbits, disbelieves entirely in its existence.[¶]

Fecundation in Plants.—In his enquiry into the question concerning the probable mode in which fecundation of the ovum of animals is effected, Professor Müller was led into an examination of the several theories adopted in explanation of the process of fecundation among plants; especially of those of Schleiden and Meyen. Since then, the opinion entertained by Schleiden that the extremity of the pollen-tube pushing the embryo-sac before it becomes detached from the rest of the tube, and constitutes the first rudiment of the future plant, has been opposed by Professor Amici,* the celebrated Italian botanist, to whom we owe the discovery of the emission of tubes by the pollen grains. From observations made on the *Cucurbita Pepo,* Amici appears to have clearly ascertained that, although the extremity of the pollen-tube enters the nucleus of the ovule to a certain depth, yet, it never penetrates the embryonic sac; and he thinks it probable that the contents of the sac are fecundated by an absorption through its membranous wall of the impregnating fluid of the pollen-tube, which is situated in the immediate neighbourhood of the sac, or even on its external surface. As other reasons against the supposition that the extremity of the pollen-tube itself becomes the embryonic vesicle from which the embryo is formed, he observes, that this vesicle exists previous to the fecundation of the ovule, and that, after fecundation, its development commences at the opposite point to that at which the pollen-tube exercises its influence. Moreover, the true embryo of the plant may be distinctly recognised before it has acquired a diameter equal to that of the pollen-tube from which it has been supposed directly to spring. His investigations, likewise, into the mode of fecundation as pursued in the Orchidaceæ, have shewn him that in these plants also, the extremity of the pollen-tube is not converted into the embryo.

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[*] Entwickl. des Hunde-Eies, p. 30.

[†] De la Fécondation, p. 35, *et seq.;* de l'Evolution Spontan. p. 370.

[‡] De l'Evol. Spont. p. 416.

[§] Philosophical Transactions, 1840, p. 533; and 1843, p. 33. In the latter place Dr. Barry states that he has twice distinctly observed several spermatozoids within the zona pellucida of ova from the rabbit.

[||] Müller's Physiology, p. 1497, and fig. 166 D.

[¶] Entwickelungs-gesch. des Hunde-eies. p. 17.

M. Tulasne†, on the other hand, from the examination of three species of *Veronica* and other plants, expresses himself as favourable to Schleiden's opinion. He states, that he has many times observed the pollen-tube to penetrate the embryo-sac, and this apparently by perforation. At no period has he been able to detect any thing which could be called an embryonic vesicle. He observes, that when the embryo-sac commences to enlarge, the plastic matter which it contains becomes developed into cells from the circumference towards the centre. During the early part of this cell-forming process, the pollen-tube within the embryo-sac remains apparently unaltered, and filled with grumous-looking material. Shortly, however, this material breaks up, and the tube which contains it becomes divided by a number of transverse septa into so many cells, which divide and subdivide: and then, in the midst of the resulting mass, the embryo appears. An opinion rather favourable to the penetration of the pollen-tube into the embryo-sac in the ovulum of *Avicennia,* has also been expressed by the late Mr. Griffith.‡

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* An. des Sc. Nat. Avril, 1847.

† Comptes Rendus, 14 Juin, 1847, p. 1060.

‡ Transactions of the Linnæan Society, vol. xx. 1846, p. 1—6.

RECENT ADVANCES

IN THE

PHYSIOLOGY OF DEVELOPMENT.

OF THE CHANGES IN THE OVUM PREVIOUS TO THE FORMATION OF THE EMBRYO.*

Under this head, it is proposed to bring together all the new facts relating to the subject, which have been derived from observations made on the invertebrate, as well as on the different classes of vertebrate, animals.

The most important subject for consideration, will be the division and subdivision of the yolk. Before entering upon this topic, however, it is necessary to inquire whether the ovum does not, immediately before, or immediately after, its extrusion from the ovary, undergo other changes previous to the manifestation of the remarkable phenomenon of spontaneous cleaving.

Changes in the germinal vesicle and germinal spot.—Dr. Barry stated, that, previous to the discharge of the ovarian ovum, the germinal spot returns to the centre of the germinal vesicle, and the germinal vesicle to the centre of the ovum; and that the germinal vesicle is not dissolved, but that while it and the germinal spot undergo the changes of place just mentioned, a peculiar process of cellular development occurs, which ends in the formation of two cells in the centre of the yolk, which have an important destination in reference to the formation of the embryo.† With reference to these various points, however, both M. Bischoff and Mr. Wharton Jones think that Dr. Barry's statements are erroneous. Bischoff describes the yolk of an ovarian ovum after coitus, as being unchanged in its characters, with the single exception of being fuller and more dense: it is still granular as before, and does not possess the layers of nucleated cells described by Barry. He thinks also, and in this opinion he is supported by Mr Wharton Jones, that the movement of the germinal vesicle and germinal spot from the surface to the centre of the ovum, could not possibly be observed even if they took place. Moreover, he is led by his observations to the conclusion that, contrary to Dr.

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* Book the Eighth, section i. p. 1508 of Müller's Physiology.

† Third Series of Researches in Embryology in Philosoph. Transact. 1840.

Barry's opinion, the germinal vesicle does really cease to exist (as indeed, observers before Barry had generally supposed), very soon after coition.* But, at the same time, he thinks that it does not always disappear before the ovum leaves the ovary.† In many cases it cannot be discerned in the ovarian ovum several hours after the coitus; and mostly, not when the ovum has entered the Fallopian tube. But, in other cases, it is often discoverable many hours after coitus, both in the ovarian ovum and even in ova which have passed into the Fallopian tube. It is, however, invariably dissolved before the commencement of the other metamorphoses of the yolk, presently to be described.‡

It is worthy of remark, that in those intestinal worms of which the ova are very transparent, Kölliker § distinctly observed, that there was a period during which the germinal vesicle was no longer to be seen, although the development of cells, preparatory to the formation of the embryo, had not yet commenced. And, in these instances it appeared to him, that the germinal spot disappeared before the germinal vesicle.

Professor Wagner,|| on the other hand, seems to agree with Dr. Barry in respect of the fate of the germinal vesicle. For he says that, although, owing to the difficulty of the subject of investigation, he has not arrived at any absolutely conclusive result, yet he regards it as a certain fact, that within the germinal vesicle the germinal spot gives rise to new generations of cells which grow with great rapidity, and eventually cause the solution or destruction of the parent-cell, or germinal vesicle. He states, that he has distinctly witnessed this process of cell-formation by the germinal spot in the ova both of frogs and Mammalia.

The observations of M. Vogt on Alytes Obstetricans,¶ are rather in favour of the view entertained by Barry and Wagner. For he states, that when the ova of this batrachian approach maturity, the germinal spots increase in number, and that when the vesicle is burst by pressure, they escape in the form of transparent vesicles, which, in ova mature enough to leave the ovary, often amount to as many as forty. Moreover, he observed, that in ova which had been discharged from the female and fecundated only a few hours, the germinal vesicle, which before was visible even to the naked eye, could now by no means be discerned, and that the germinal spot also seemed to have disappeared, though, on farther search, several

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* Entwickl. der Säugeth. und des Menschen, p. 42.

† Ibid.

‡ The germinal spot, however, Bischoff supposed, from what he observed in the rabbit, not to be dissolved, like the germinal vesicle, but to be set free, and subsequently to undergo peculiar changes to which reference will again be made. Recently, however, Bischoff has had reason to doubt the correctness of the above view, for in two cases he could not detect any spot in the perfectly isolated germinal vesicle of bitches' ova. (Entwick. des Hunde-eies, p. 42.)

§ Müller's Archiv. 1843. p. 77.

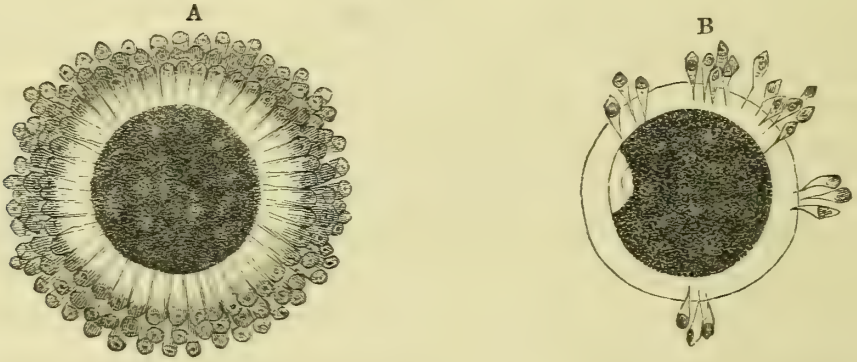
|| Lehrbuch der Physiologie, Second edit. p. 53.

¶ Untersuchungen über die Entwickelung der Geburtshelfer-Kröte. Solothurn. 1841. p. 4.

small clear vesicles, exactly similar to those mentioned as being formed within the germinal vesicle, were observed scattered through the yolk. It appears, therefore, that the fate of the germinal vesicle with its germinal spot, is still matter of uncertainty.

Changes in the tunica granulosa.—Both Barry and Bischoff have observed, that the cells of the membrana granulosa of the ovisac, which immediately surround and adhere to the ovum, undergo a peculiar change of form about the time at which the ovum is destined to leave the ovary. They become club-shaped, their pointed extremities being attached to the zona pellucida, so as to give the ovum a stellate appearance (see fig. 5). The club-shaped extremity of each cell contains a distinct nucleus, and Barry states, that in place of this nucleus, a pellucid space is afterwards seen; that a young cell succeeds, and that subsequently, the whole cell becomes filled with other cells. Bischoff, however, has seen none of the latter appearances. But he has observed, that when the ovum enters the Fallopian tube, these cells lose their spindle-or club-like shape, and become quite round. In the bitch, they continue to invest the ovum in this round shape throughout the whole tract of the Fallopian tube—disappearing only when the ovum reaches the uterus [†]—but in the rabbit, they wholly disappear at its very commencement.

Fig. 5.[*]



Contraction of the Yolk. Formation of the Chorion.—Besides the disappearance of the germinal vesicle, and, in the rabbit, the disappearance also of the cells of the membrana granulosa, it is observed, according to Bischoff, that in the upper part of the Fallopian tube, the yolk no longer completely fills the zona pellucida, but that a clear fluid collects between them, and that the contour of the yolk becomes defined by a dark line. This change Bischoff ascribes to a contracted and consequently more dense condition of the yolk, the granules composing which now adhere together so firmly, that when the yolk is broken down with a needle, they do not become diffused through the surrounding fluid, as they would have done previously.

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[*] Fig. 5. A. An ovarian ovum from a bitch in heat, exhibiting the elongated form and stellate arrangement of the cells of the discus proligerus or membrana granulosa around the zona pellucida. B. The same ovum after the removal of most of the club-shaped cells.

[†] Entwickel. des Hunde-eies, p. 41.

As the ovum approaches the middle of the Fallopian tube, it begins to receive a new investment, consisting of a layer of transparent albuminous or glutinous substance, which forms upon the exterior of the zona pellucida. It is at first exceedingly fine, and, owing to this and to its transparency, it is not easily recognised; but as the ovum reaches the lower part of the Fallopian tube, this new investment acquires considerable thickness, and shortly begins to assume the characters of the chorion, into which it, together with the zona pellucida, is subsequently converted.* At this part of its transit along the Fallopian tube, the ovum remains still unchanged in structure, and no alteration, beyond increased thickness, is perceived in the zona pellucida. A remarkable phenomenon has, however, been noticed by Bischoff, about this time, namely, the rotation of the yolk within the zona pellucida—a phenomenon produced, he says, by the action of vibratile cilia, situated upon the surface of the yolk. This curious observation has been described in a note at page 1564 of Müller's Physiology.†

The changes which the mammalian ovum undergoes in its passage through the second half of the Fallopian tube, consist in the further formation of the chorion, and in the peculiar process of cleaving of the yolk, which will now be discussed. The development of the chorion, will be considered at a future page.

Division and subdivision of the yolk.

This process has been long known to occur in the amphibia and fishes and some invertebrate animals. And observations of Dr. Barry, relative to the rabbits' ovum, seemed to shew that a similar change occurs in the ovum of mammiferous animals. This is now known with certainty to be the case. The exact nature of the process is, however, still involved in doubt, and very different opinions respecting it are entertained by different physiologists.

The phenomena are observed with more difficulty in the higher than in the lower animals. Hence, it seems desirable to detail those which have been recently investigated under favourable circumstances, and with great ability, by Professor Kölliker ‡ and Dr. H. Bagge,§ in many of the Invertebrata, before noticing the corresponding changes which have been observed to take place in the ova of Mammalia.

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* This deposit of albuminous matter around the ovum, first described by Mr. Wharton Jones, appears to have been yet observed only in the rabbit; no such deposit takes place around the ovum of the bitch (Bischoff, l. c. page 46), in which animal the chorion is formed from the zona pellucida alone.

† The rabbit appears to be the only mammalian animal in whose ova this rotation of the entire mass of the yolk, previous to cleavage, has been observed. Bischoff has never detected it in the bitch's ovum, but the Fallopian tube in these animals is so thick and opaque, that the phenomenon might occur without being perceived (Entw. des Hunde-eies, p. 46).

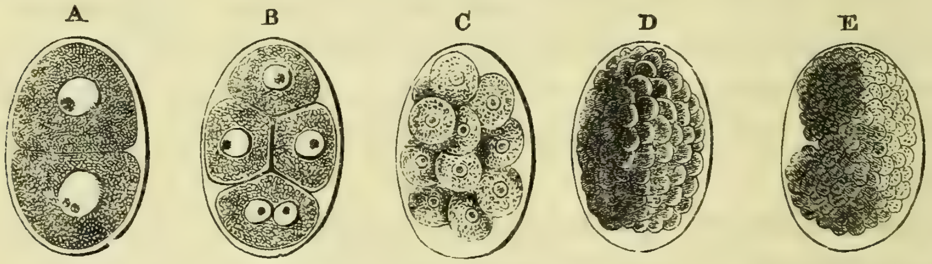
‡ Entwickelungs-geschichte wirbellöser Thiere, Müller's Archiv. 1843, p. 68; and Entwickl. der Cephalopoden, Zurich, 1844.

§ De Evolut. Strongyli auric. et Ascarid. acum. Vivip. Diss. Inaug. Erlangæ, 1841.

In the Invertebrata.—From the investigations of the former of these observers, it would appear, that the early structural changes undergone by the substance of the impregnated ovum, are of several varieties in the different invertebrate animals; but that, so far as has yet been ascertained, these varieties are referable to three principal types. In the first type, the whole substance of the yolk undergoes the process of division and subdivision. In the second, the process is confined to a portion of the yolk. And, in the third type, the yolk does not take any part in the process, but certain transparent nucleated cells, arising in its interior, undergo multiplication in the same manner as the yolk itself in the former varieties: the substance of the yolk in this third type being gradually absorbed during the process.

I. The first of these types is exemplified in the ova of three species of Ascarides, namely, Ascaris nigrovenosa, A. acuminata, and A. succisa.* Kölliker † states, that as soon as the mature ova of one of these worms reach the fundus of the uterus, the first signs of impregnation are manifested by the disappearance of the germinal vesicle, and a diminution in the consistence of the yolk, the granules of which adhere together less firmly than before. Shortly after this change, a new nucleated cell appears in the centre of the yolk, which then again acquires a closer texture, a smaller circumference, and a more definite outline. After a time, two cells instead of one are perceived in the interior of the yolk, and soon the yolk itself divides into two halves, each of which contains one of the cells in its centre (fig. 6, A). Then, again, each of the two cells is replaced by two others, and the substance of the yolk becomes divided into four

Fig. 6. ‡



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* The development of these Entozoa was described by Von Siebold (Burdach's Physiologie. Second edition, vol. ii.), but has been more recently and more accurately investigated by Bagge and Kölliker in the essays above alluded to.

† Müller's Archiv. 1843, p. 103.

‡ Fig. 6. Cleaving of the yolk after fecundation. A. An ovum, the yolk of which is divided into two equal portions; the upper portion contains a cell with a large nucleus, the lower, a similar cell with two small nuclei. B. An ovum, of which the yolk is divided into four masses, three of which possess a single nucleated cell, the fourth, two such cells. C. An ovum, the globular masses of whose yolk amount to sixteen, in each of which a

masses, corresponding to the four cells which they enclose within them (B). This process of division, by which each cell, and consequently each mass of yolk-substance, is resolved into two others of half the size of the original, is repeated until the yolk is converted into an oval mass composed of globules, in the interior of each of which, the existence of a nucleated cell can be distinctly discerned (C). Beyond this point, however, the cells can no longer be recognised, though the process of division continues, and the globular masses become smaller and smaller (D, E), until, eventually, they begin to be moulded into the form of the young worm, in the construction of which they all take part.

Such is a general outline of the process as it occurs among these varieties of Ascarides, and has been observed also among several other invertebrate animals. There are certain questions, however, which present themselves for solution in the further consideration of it. These are—

What is the mode of origin of the first cell seen within the yolk after the disappearance of the germinal vesicle?

What is the mode of multiplication of this cell?

How is the division of the yolk produced?

Are the different segments of the yolk to be regarded as cells?

Neither Bagge nor Kölliker observed any facts which afford an answer to the first question. For they were unable to perceive the first embryonic cell within the yolk until it was completely formed. This much, however, seems certain, that the cell is not developed from the germinal spot or nucleus of the germinal vesicle. For in the perfectly transparent ova of Ascaris dentata, Kölliker satisfied himself that the germinal spot as well as the germinal vesicle invariably disappeared, and that a certain period elapsed between their disappearance and the formation of the first embryonic or germinal cell.

With regard to the mode of multiplication of the cells of the yolk, Bagge and Kölliker are at issue. Bagge, who appears not to have observed that the cells possess nuclei, represents them as undergoing division much in the manner of the fissiparous generation of polygastric animalcules. But Kölliker has shewn that each cell is nucleated, and that sometimes one large cell contains two small nuclei in place of one of twice the size. And as he has observed in other Entozoa that the same cells multiply by the development of two young cells from the two halves of the divided nucleus within the parent cell, which then disappears, he draws the fair inference that the same process occurs in these Ascarides also. A similar opinion is entertained also by Dr. Sharpey.*

It would seem that the division of the yolk is a consequence of the

nucleated cell is clearly discernible. From Ascaris nigrovenosa. (After Kölliker.) D. and E. are representations of ova from Ascaris acuminata, shewing subsequent steps in the process of division described in the text. (After Bagge, op. cit.)

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* Quain's Anatomy. Fifth edition, p. l.

multiplication of the cells. For, it is not until two cells have appeared in place of the one which previously occupied the mass of the yolk, that the latter begins to undergo division. Kölliker therefore regards the division and subdivision of the yolk, as the consequence of an attractive force exerted by the germ-cells on the vitelline or yolk-substance.* And Dr. Sharpey † remarks, that the shrinking of the granular mass of the yolk around the first central cell, is in harmony with this view. Dr. Sharpey also mentions the fact, that on one occasion while he was examining the ova of one of these Ascarides, at the time when one of the large segments into which the yolk is first cleft, divided itself into two portions, he observed a very obvious heaving motion among the granules throughout the whole mass; then ensued a constriction at the circumference, which, proceeding inwards, soon completed the division.‡

Kölliker thinks that the earlier divisions of the yolk cannot be regarded as cells, for they appear to him not to be enveloped with a membrane. Dr. Sharpey,§ on the other hand, is disposed from his observations on the ova of Ascaris, to admit the existence of an enveloping membrane, and consequently he regards these larger, as well as the later and smaller subdivisions of the yolk, as complex cells, analogous in their structure to the unimpregnated ovum, and to the nucleated globules of the nervous system.||

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* L. c. p. 108.

† Loc. cit.

‡ In relation to this question concerning the cause of the division of the yolk, may be also mentioned the results of some observations recently made by Vogt on the development of the Molluscous Gasteropods. (Ann. des Sci. Nat. 1846. Zoologie, p. 23, *et seq.*) According to this embryologist, the yolk of the ovum of Acteon viridis (on which his observations were almost exclusively made) consists, immediately after impregnation, of a gelatinous substance containing numerous minute granules, and having in its centre a round transparent vesicle appearing as a clear space. Shortly afterwards the vitellary mass divides into two equal portions, in the centre of each of which is contained a clear vesicle, like that before observed in the centre of the yolk itself. But, contrary to the above-stated opinion of Kölliker, and to that of most other embryologists, Vogt believes that, at least in Acteon, the division of the vitellary mass, instead of being a consequence of the multiplication of the central vesicle, precedes, and is the cause of, the latter phenomenon. The only evidence, however, on which this opinion appears to be based is, that in one instance Vogt observed an ovum in which one of the two portions into which the yolk was dividing was somewhat smaller than the other, as if of more recent formation, and did not contain a vesicle.

§ Quain's Anatomy, p. l.

|| According to Vogt's observations, the very earliest divisions of the yolk-mass, in the ovum of Acteon, are unprovided with an enveloping membrane, yet, by the time the number of segments has amounted to twenty-four, evidences of an investing membrane around each may usually be observed. (Further observations on this subject will be made when considering the process of division and subdivision of the yolk as it occurs in the mammiferous ovum.) A remarkable peculiarity has also been observed by Vogt in the products of the division of the yolk in this animal. The first two divisions of the vitellary mass subdivide as in the ova of other animals, and produce four equal-sized spheres, arranged together in a crucial form, and each possessed of a central transparent vesicle. But in the

II. In the second variety of the process of yolk-cleaving, only a part of the yolk is the seat of this phenomenon. The only invertebrate animals in which this variety has been observed, are the Cephalopods, and a description of the process as it occurs in the ova of these animals has been furnished by Kölliker from observations on the Sepia.* In the unimpregnated ovum of this animal, as in those of fishes, and Alytes obstetricans,† the germinal vesicle is situated at one part of the surface of the yolk, instead of being imbedded in the centre, as it is in most other cases. And the process of cleaving commences in the situation of this vesicle, and in the Sepia, is confined to its immediate neighbourhood. Shortly after the disappearance of the germinal vesicle, consequent on fecundation, a slight elevation of the yolk appears at that part of the surface where the vesicle was situated. This elevation soon divides into two prominences, within each of which is contained a nucleated cell, surrounded by granular matter. The two prominences are shortly divided into four, and then into eight, segments, each containing a cell surrounded by granules. These segments have the form of segments of a circular disc, all meeting with round, well-defined, prominent ends at the centre, where the nucleated or embryonic cells are situated; but at the periphery of the circle, passing, without any definite line of separation, into the yolk. At the next stage the eight segments of the circle give off at their apices eight globular segments, which form a ring within the radiating segments. Each globular segment, as well as each newly-formed apex of the radiating segments, contains an embryonic cell. All these segments then divide, so that there result sixteen radiating, and sixteen globular segments, in each of which is an embryonic cell. A new

next stage of the process, the four spherical masses, instead of dividing into eight smaller equal-sized spheres, retain, as nearly as possible, their original size, while from one surface of the crucial-shaped plane which they form, four other spherical bodies gradually arise, which, when fully formed, are about half the size of the large ones, and much more transparent, owing to the very few granules which they contain; each possesses a clear vesicle similar to that in the larger spheres. It did not appear as if these smaller masses were formed by a division of the larger spheres, for, as above stated, these latter maintained almost their original size; they seemed rather to be produced by a kind of exudation from the large masses of the more viscous part of the yolk-substance, few granules entering into their composition. After this event, the several segments of the yolk go on dividing and subdividing in the ordinary way, and the difference in size between the two above-mentioned sets of spheres shortly disappears; but throughout the whole process the divisions of the larger set remain granular and opake, while those of the small set continue to be characterized by their transparency. When the process of cleaving is complete, the former are all found in the centre of the yolk, and are accordingly named by Vogt the central spheres, while the latter are situated at the surface, and are hence termed by him peripheral spheres. From the central opake spheres, or cells as they have by this time become, he states that the central parts of the embryo are formed while the peripheral organs are developed out of the transparent spheres or cells.

* Entwickelungs. der Cephalopoden, pp. 17—40.

† Entwickel. der Geburtshelferkröte, p. 1.

ring of globules with cells is then formed, whereupon these and the radiating segments again suffer division in the direction of the radius of a circle. This process is repeated; the radiating segments meanwhile extending at the periphery, while they are shortened and narrowed at their apices by the divisions they undergo. At length these divisions reach a stage, when the apex of each radiating segment is given off together with the embryonic cell, leaving no remaining cell in the apices. When this takes place, the radiating segments disappear, or cease to be distinguishable from the rest of the yolk. Henceforward the germinal space contains only globular segments of yolk, each including an embryonic cell; the globules being smallest in the centre. Kölliker maintains that neither the earlier divisions of the yolk, nor even the last small globules, can be regarded as cells. For the segments and the first formed, larger, globules are, he says, merely hillocks of elementary granules on the surface of the yolk collected around the embryonic cells. And the small globules appear to differ from these only in their size, and in containing more granular matter. In the Sepia, as in the Ascarides, Kölliker is of opinion that the division of the yolk into segments or globules, is dependent on some attractive force, exerted by the nucleated embryonic cells upon the substance composing the yolk, and that the cells themselves multiply, as in the Ascarides, by the development of two young cells within each parent-cell.

III. The third variety of the changes which take place in the yolk in invertebrate animals, subsequently to fecundation and the disappearance of the germinal vesicle, is exemplified in the ovum of Ascaris dentata; and the observations which Kölliker* has made on the changes of the yolk in this Entozoon are of great importance, since, owing to the almost complete transparency of the ova and their coats, it is scarcely possible that any error of observation can have been committed. In these investigations Kölliker found that, for a short time after the disappearance of the germinal vesicle, the ovum is seen to contain merely the transparent fluid of the yolk, with very scanty elementary granules. But soon the first embryonic cell is developed in the centre of the yolk. This cell is quite transparent, globular, somewhat larger than the previous germinal vesicle, and has a small, pale, round nucleus attached to its wall. As the ova advance through the cavity of the uterus, this embryonic cell is replaced by two similar cells; then four such cells are seen, then eight, and so on, the cells becoming more and more numerous, and diminishing in size as they increase in number. While these cells are thus undergoing multiplication in the centre of the yolk, the yolk itself suffers no change except in quantity; it gradually disappears, being consumed, as it would seem, in the growth of the embryonic cells. These, while they multiply, occupy more and more space, for although each of the two new cells is smaller than the one which preceded them, yet the two together occupy much more space than it did. So that at length the yolk-membrane or ovum is completely filled with a mass of small cells, in which the nucleus can no longer be distinguished; and at a still later stage even their cell-like form cannot be distinguished, and the mass, which now begins to take the form of the young worm, seems to be composed merely of granules.

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* Müller's Archiv. 1843, pp. 76—85.

In this Entozoon Kölliker has distinctly observed, that the mode of multiplication of the cells consists in the development of two young cells within each of the cells of the preceding generation; the parent cell then undergoing solution and disappearing. Kölliker believes that the development of the two new cells is dependent on the previous division of the nucleus of the parent-cell, each division of the nucleus giving rise to a new cell. For in the ova of Cucullanus elegans, in which the process just described from Ascaris dentata is repeated, he has often observed cells the nuclei of which were, in some instances, elongated, in others, constricted in the middle, while in other cells there were two nuclei in place of one, these two being smaller than the single nucleus of the neighbouring cells, and situated, in some cases, close together, in others, more removed from each other (fig. 7). His opinion is made more probable also, by the fact of his having seen in ova of Ascaris dentata, two small nucleated cells enclosed within a parent-cell which had no nucleus (see fig. 8, C).

Fig. 7.*

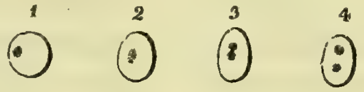
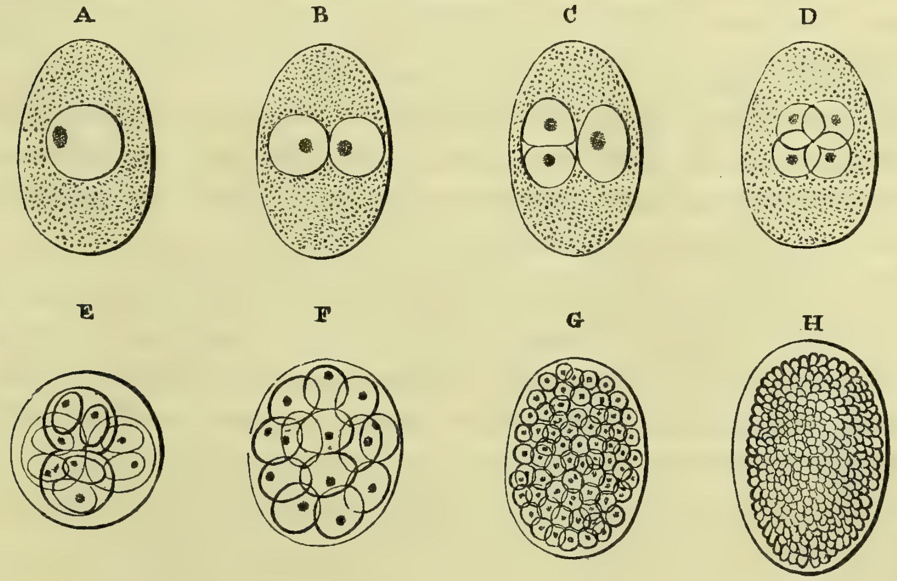


Fig. 8. †



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* Fig. 7. Cells from ovum of Cucullanus elegans, shewing supposed division of the nucleus in the manner just described. (After Kölliker.)

† Fig. 8. A, B, C, D, successive stages of the ovum of Ascaris dentata, shewing duplication of cells. E, F, G, H, ovum of Cucullanus elegans, shewing the advance of the process. (After Kölliker.)

From the preceding account of the three principal varieties of the process which intervenes between the disappearance of the germinal vesicle and the formation of the embryo, in Entozoa and many other invertebrate animals, it will be apparent, as Kölliker remarks, that the more essential part of the process is the development and multiplication of nucleated embryonic cells, which become smaller as they increase in number, and at length form the granular mass out of which the embryo is moulded. The part played by the yolk appears to be a subordinate one: the peculiar process of division and subdivision, which, in some cases, it undergoes—whether this affects its whole mass, or only a limited portion of it—being determined and regulated by the development and increase of the embryonic cells.

In Amphibia and Fishes.—It remains to inquire how far the phenomena observed in the ova of vertebrate animals agree with those which we have just been considering: and, first of all, to apply the facts with which we have become acquainted, to the explanation of the analogous process in Amphibia and Fishes.

That variety in the process which consists in the whole yolk undergoing division and subdivision, was discovered long since, in the ova of frogs, by Prévost and Dumas,* and afterwards described with great accuracy by Von Baer.† Baer, however, seems to have entertained no suspicion that the segments of the yolk are other than solid homogeneous masses of the yolk-substance. Rusconi,‡ in criticizing Baer's account of the process, remarked, that there were cavities in each of the eight masses into which the dark half of the yolk divided, and was probably led to make this remark by seeing the transparent embryonic cells. But Bergmann § first announced that each of the masses of the yolk contained a transparent body, which he supposed to be a solid nucleus.

From these observations, though imperfect, the most natural inference is, that the process described by Bagge and Kölliker, as taking place in the ova of Strongylus auricularis, and Ascaris nigrovenosa, and acuminata, takes place also in the frog, and that the division and subdivision of the yolk is dependent, in the latter animal, as in those Entozoa, on the development and multiplication of embryonic cells. Kölliker‖ indeed states, that he has seen nuclei in the vesicles which occupy the centre of the segments of the yolk in the frog's ovum. The earlier statements of Reichert,¶ too, respecting the structure of the yolk at the end of the process of cleaving are also reconcilable with that view. The smaller corpuscules, he describes, may be the last generation of the embryonic cells, still surrounded by

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* Müller's Physiology, p. 1508. † Ibid. p. 1509, and fig. 168.

‡ Müller's Archiv. 1836, p, 218.

§ Müller's Physiology, p. 1509 note; and Müller's Archiv. 1841, p. 89.

‖ Entwickelungs-geschichte der Cephalopoden, p. 121.

¶ Müller's Physiology, p. 1512.

some of the yolk-substance. The larger corpuscules may, in some cases, be segments containing each an embryonic cell.*

It must be mentioned, however, that Bischoff has never been able to detect any nuclei in the transparent corpuscules or vesicles contained in the segments of the yolk of the frog's ovum, and, therefore, does not regard them as true cells. In other of the Amphibia, as Alytes obstetricans, and also in fishes, the process of cleaving affects only a part of the yolk, as in the second type described in the invertebrate animals. The external characters of the process as witnessed by Rusconi in the tench (Cyprinus tinca), are described at page 1510, of Müller's Physiology. The more intimate nature of the changes have been investigated by Vogt, in Alytes† and Coregonus palæa‡ (one of the salmon tribe). In Alytes, the cleaving affects only one half of the ovum, and, according to Vogt, only the surface of the yolk. For, at that stage of the process, when the surface is mulberry-like, the different segments, though rounded and defined towards the exterior, are towards the interior uninterruptedly continuous with the general substance of the yolk, just as is the case with the earlier segments of the ovum of Sepia. The segments contain (for the most part), each, a transparent round vesicle; and after the process is completed, and previous to the appearance of the embryo, the whole yolk is composed of cells, in the centre of each of which, a similar transparent vesicle, as a nucleus, is

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* Reichert's later account (Müller's Archiv. 1841, p. 523) of the process of cleaving in the frog's ovum does not accord with the facts observed by other anatomists. The opinion which he advances is, that the smaller corpuscules which he finds composing the ovum at the end of the process, and regards as cells, all exist completely formed before impregnation takes place. Not, however, that he regards these cells as existing in a free state, but every two or three included within larger cells, and these again in still larger, and so on: the cells of each set enclosing within them smaller cells, and being themselves enclosed within larger, and all being contained within two large cells, which, in their turn, are held together by an investing membrane forming one large cell. The process of cleaving thus consists, according to Reichert, simply in the liberation, first of the two large cells, and then of each successive set of enclosed cells, by the solution of the including cells, till at length the smallest nucleated cells, destined to form the embryonic structures, are set at liberty. The facts really observed on which this hypothesis is based, seem to have been very few and very inconclusive. In a still more recent account (Muller's Archiv. 1846, p. 196), of the process of cleaving in the ovum of Strongylus Auricularis, Reichert modifies this opinion, and admits that the process really consists in the formation of successive crops of new cells. Even the largest segments of the ovum, he (like Dr. Sharpey) regards as true cells, and he states that in the process of duplication the nucleus of each such cell first breaks up into a number of oil-like particles which mix with the granular contents of the cell, that then this mixed mass gradually divides into two equal portions, each of which becomes invested with a distinct membrane; and that, subsequently, a clear vesicular body or nucleus forms in the centre of each. When fully formed these two cells are liberated by the solution of the parent cell-wall, and then undergo a similar process of division; the nucleus of each invariably disappearing before the division commences.

† Entwickelungs-gesch. der Geburtshelferkröte.

‡ Histoire Natur. des Poissons d'eau douce, by M. Agassiz. Tome i. 1842.

situated: the contents of each cell consisting of the granules and lamellæ of stearine, which previously constituted the yolk. These facts accord with the observations of Kölliker, on the sepia and intestinal worms. But other parts of Vogt's description cannot be reconciled with Kölliker's views: for instance, the statements that the cleaving of the yolk is produced by folding in of the yolk membrane: that some of the segments have no cell-nucleus, while others contain several: and that the formation of the cells last described, is not coincident with the cleaving, but begins after the cleaving-process has wholly ceased—a space of time intervening in which nothing like cells exist. Vogt believes, too, that the transparent cells which are contained in the segments of the yolk, are multiple germinal spots, which remain when the germinal vesicle, in consequence of impregnation, disappears, and which exist in the yolk before the process of cleaving commences (see page 63). Between Vogt's account of the process in Coregonus, and Kölliker's description of the division and subdivision of the yolk in Sepia and other Invertebrata, there is much apparent discrepancy. Kölliker, however, thinks that they may be reconciled. As there is, however, much that is indefinite in Vogt's description, further consideration of it need not be entered into here. It may be remarked, however, that Vogt is of opinion, that here also the germinal spots play an important part in bringing about the changes in the yolk, which precede the formation of the embryo.

In Birds, nothing like a cleaving of the yolk has hitherto been observed. It is supposed that the extent of the yolk implicated in the process may be very limited. It may be, perhaps, that the process does not affect the yolk itself, but consists solely in the development and multiplication of embryonic cells, in the central cavity of the yolk, such as is described by Kölliker in Ascaris dentata and Cucullanus elegans (see page 71, and fig. 8), but without the simultaneous absorption of yolk substance, such as takes place in those Entozoa.*

In Mammalia.—Lastly, the nature of the process which takes place in the ova of Mammalia must be inquired into.

The changes which the yolk of the rabbit's ovum undergoes, during its transit through the Fallopian tube, have been investigated by Dr. Barry and Professor Bischoff:† and, more recently, the analogous changes which occur in the bitch's ovum have also been examined by Bischoff.‡ Dr. Barry's earlier observations were given at page 1565 of Müller's Physiology. His later Researches § afford results, which in respect to the more im-

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* M. Coste (Comptes Rendus, 5 Avril, 1847,) states, however, that he has observed the process of cleaving in the ovum of birds during its passage along the oviduct; and he remarks that it is limited to that portion of the yolk which constitutes the cicatricula.

† Entwickelungs-geschichte des Kaninchen-eies, 1842.

‡ Entwickelungs-geschichte des Hunde-eies, 1845.

§ Third Series, Philosophical Transactions, 1840.

portant and trustworthy points, are confirmatory of these earlier ones. And if merely the figures which he gives be examined (see the figures copied in Müller's Physiology, page 1567, and the plates in Dr. Barry's second and third Series of Researches on Embryology),* it will be seen that the appearances in the rabbits' ova taken from the Fallopian tube, agree in the most important points with the account of the first type of the process of cleaving observed by Bagge and Kölliker, in the ova of the three varieties of Ascaris. For Dr. Barry not only saw the division and subdivision of the yolk, but he also distinguished a pellucid space or nucleus in each of the segments, and he seems to have observed the development of two embryonic cells within the first single cell which takes the place of the germinal vesicle in the yolk, the subsequent development of two younger cells within each of these, and the continued repetition of this mode of multiplication.

The description of the process given by Bischoff, as he witnessed it in the ova of the rabbit and of the bitch, is generally similar to Bagge's account of what he observed in the Strongylus auricularis. When, in these Mammalia, the ovum has passed the middle of the Fallopian tube in its transit to the uterus, the yolk, which was previously one compact uniform mass, begins to be resolved into a number of smaller spheroidal masses; first into two, then into four, then eight, then sixteen, and so on (see fig. 9). Each segment contains a transparent vesicle, which is seen with difficulty, especially in the bitch's ovum, on account of its being enveloped by the yolk granules, which adhere closely to its surface. This vesicle, Bischoff says, when liberated from the surrounding yolk granules, most nearly resembles a fat or oil-globule. He has never been able to detect a nucleus in it, though he has repeatedly and carefully examined it for this purpose in the ova of the rabbit and the bitch. Bischoff, therefore, cannot subscribe to the opinion, that the central vesicle of each globular segment of the yolk is a nucleated, or embryonic, cell. Neither does he regard the globular segments themselves as cells, for he states that neither in the rabbit nor in the bitch can any investing membrane be discerned. He considers them as simple aggregrations of yolk substance around the central body or vesicle, such as the earlier divisions of the ova of Ascarides nigrovenosa and acuminata and those of Sepia are, according to Kölliker.

It will be seen that the mode of division and subdivision of the yolk of the mammal's ovum, agrees in its principal and more obvious features with the first type described at page 66, as occurring in invertebrate animals. The process cannot, however, be regarded as essentially the same in the two cases, until the central vesicles of the segments in the mammal's ovum shall be shewn to be nucleated cells, the nuclei of which multiply by division, and thus determine the multiplication of the cells, two new

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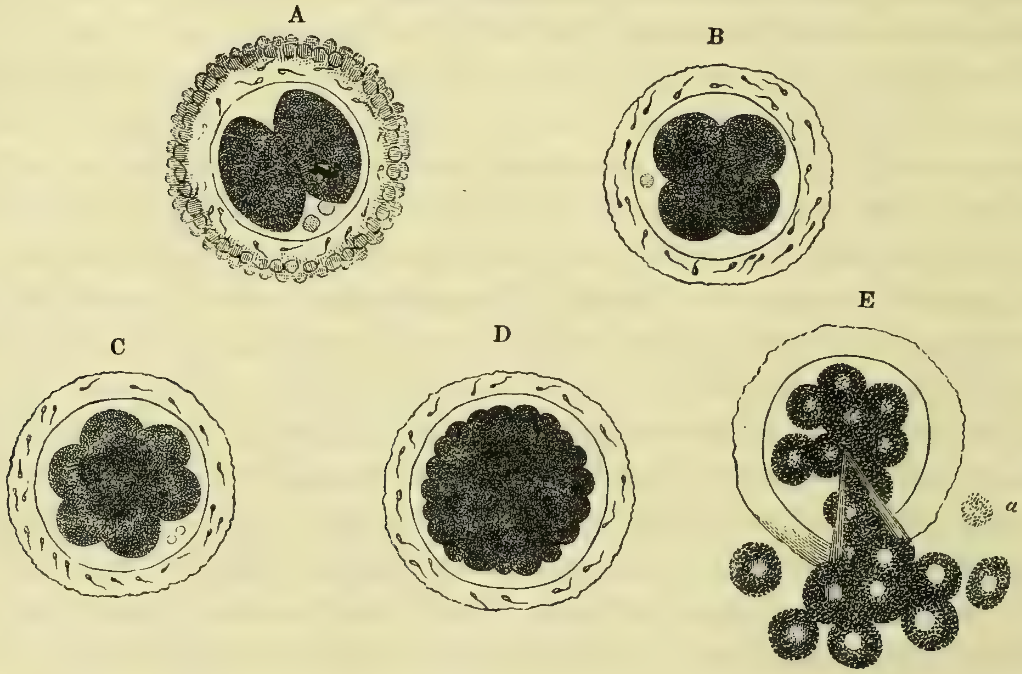
* Philosophical Transactions, 1839 and 1840.

cells being produced within each parent-cell. But no observer has yet seen a nucleus in any of the central vesicles of the yolk segments of the ovum of Mammalia. Bischoff remarks, however, that these vesicles, though not nucleated, evidently play the part of nuclei in the spherical yolk segments, and that the aggregation of the yolk substance into spherical segments must be due to a kind of attraction exerted by the vesicles. How the multiplication of the vesicles takes place, by which the subdivision of the yolk is effected, he cannot decide. But he sees no positive objection to the belief that they themselves multiply by division.†

*Fig. 9.**



Changes in the ovum subsequent to the process of cleaving.

With respect to the changes which occur in the ova of *invertebrate animals* after the completion of the process of cleaving, or analogous processes, little need be added to what has been already said. For

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* Fig. 9, A. Ovum of a bitch, from the Fallopian tube, half an inch from its opening into the uterus, shewing the zona pellucida with adherent spermatozoids, the yolk divided into its first two segments, and two small granules or vesicles contained with the yolk in the cavity of the zona. B. Ovum of a bitch from the lower extremity of the Fallopian tube: the cells of the tunica granulosa have disappeared: the yolk is divided into four segments. C. Ovum of bitch from the lower extremity of the Fallopian tube, in a later stage of the division of the yolk. D. An ovum from the uterus: it is larger, the zona thicker, and the segments of the yolk are very numerous. E. Ovum from the lower extremity of the Fallopian tube burst by compression: the segments of the yolk have partly escaped, and in each of them a bright spot or vesicle is visible.

† Bischoff, Entwickelungs-geschichte des Hunde-eies, pp. 45, 46.

in those invertebrate animals, such as certain Ascarides and other Entozoa, in which the whole yolk is included in the cleaving or other process which ensues shortly after fecundation, the embryo is at once formed out of the entire mass of particles into which the yolk is resolved at the completion of this process. And in those, such as the Sepia, in which the process of division is confined to a limited part of the surface of the yolk, the only notable change which ensues between the completion of this process and the first appearance of the embryo, is the arrangement of the ultimate segments at the surface of the yolk into a double membrane, which is analogous to the germinal membrane in the ova of other animals. The inner layer of this membrane constitutes the inner and outer yolk-sac, while from the outer layer is produced the embryo and its several organs.*

In *amphibia* and *fishes*, however, certain other changes occur during this period which are deserving of notice.

The most important contribution of late years to this portion of the subject of development, has been furnished by Vogt.† In his opinion, the formation of cells in the yolk does not commence until after the completion of the cleaving process. When this process has entirely ceased and the ovum of Alytes has regained its former smooth exterior, the central part or yolk-nucleus (Dotterkern) is observed to have a darkish yellow colour, while the external cortical part, which is composed of molecular corpuscules, among which are scattered a few free germinal cells or vesicles (see page 63), has a whitish aspect. After a period of apparent rest ‡ succeeding the completion of the cleaving process of the yolk, the development of cells commences at that part of the cortical portion of the ovum at which the embryo subsequently appears, whence it extends over the remaining surface of the yolk and towards the interior. This formation of cells, according to Vogt's account, takes place by the production of an enveloping membrane around each of the germinal cells or vesicles already existing in the cortical substance. A portion of the granular material of the ovum is included between each germinal cell and the newly-formed investing cell-membrane, and constitutes the nutritive contents of the yolk-cell. It would seem, also, that new germinal cells are being continually formed, and then, by the above process, developed into yolk-cells. The first set of yolk-cells which are produced, accumulate at the surface of the ovum, and adhere together so as to form a membranous layer, which gradually extends over the entire surface, and increases in thickness as fresh quantities of cells are deposited on its interior.

Within the substance of this membrane is subsequently developed the earliest trace of the embryo, namely, the primitive groove, bounded by the two lateral masses, the laminæ dorsales. After the formation of yolk-cells has proceeded to a certain extent in the cortical part of the ovum, a similar process commences in the central portion. In this part of the ovum, however, there are originally no germinal cells; and it would seem, according to Vogt,* that at this period clear transparent cells, exactly similar to the germinal cells, are developed here; and that then an investing membrane forms around each of them, and thus produces so many yolk-cells in the same manner as those of the cortical part are formed. The cells of the central part of the ovum differ, however, from the cortical ones, in being larger, of an irregular form, and possessing stearine, instead of granular matter, as their contents. During the early period of the cell-formation in the central part of the ovum, gradual transitions in form and other characters, from the cortical to the central cells, may be perceived as the ovum is examined from without inwards. But at a later period the cortical cells become more and more distinctly separated from the central ones, and eventually constitute a perfectly distinct layer, which can be completely separated from the central portion of the ovum, without injury to either. On comparing the description furnished by Reichert† of the composition of the frog's ovum subsequent to impregnation, with Vogt's account as given above, it will be observed that, at least with regard to the variety in size of the cells of the yolk, a close similarity exists between them. But concerning the nature of these two kinds of cells or corpuscules, the changes which subsequently ensue in them, and the relative share possessed by each in the formation of the embryo, considerable discrepancy is observed in their opinions. By Reichert it was assumed that the large central cells, which at first are unprovided with nuclei, subsequently became nucleated, that young cells are then developed within them, and that, in proportion as they approach the periphery of the yolk so do the young corpuscules within increase in size; and eventually the membranous wall of the parent-cell disappears, while the small liberated cells constitute the formative mass out of which the several parts of the embryo are developed. And this, he considers, goes on until the whole of the large yolk-cells are resolved into broods of smaller cells; and the nearer these larger cells are to the centre of the yolk, the later are they in the production of young cells in their interior. The whole of this view, however, is contradicted by Vogt,‡ who observes that, at least in the ovum of the toad, no trace of young cells contained within parent-cells can be detected at the centre or any other part of the substance of the yolk; and he considers that the young cell which Reichert figures within a larger one§ is simply the germinal cell, around which the larger yolk-cell has formed, in the manner already described. In Vogt's opinion, as already expressed, the peripheral

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* Kölliker, Entwickelungs-geschichte der Cephalopoden, p. 61.

† Entwickelungs-geschichte des Geburtshelferkröte, and Histoire Naturelle des Poissons, par M. Agassiz, t. i.

‡ Entwick. des Geburtshelferkröte, p. 10.

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[*] Entwick. des Geburtshelferkröte, p. 11. [†] Müller's Physiology, p. 1512.

[‡] Entwick. des Geburtshelferkröte, pp. 34—40.

[§] See fig. 170, p. 1513, Müller's Physiology.

cells of the yolk are developed as primary and independent structures, just as the central cells are; and the only probable way in which the latter may contribute to the production of subsequent sets of the peripheral cells, is by providing the nutritive material, or intercellular substance, out of which fresh quantities of new cells may be formed to supply the place of those consumed in the successive development of the several parts of the embryo. In the ovum of the young salmon, also, there is complete absence of anything like the production of young cells within larger ones. Indeed the yolk of the salmon's ovum appears to consist almost entirely of a clear gelatinous homogeneous fluid, without cells or corpuscules of any kind; the only trace of cells being found at the periphery in the immediate neighbourhood of the developing embryo.*

The difference in the opinions, therefore, of these observers, concerning the nature and ultimate condition of the two sets of cells found in the yolk soon after the completion of the cleaving process, appears to consist essentially in this: that, whereas, Reichert regards the smaller peripheral cells as the offspring of the large central ones, and is of opinion that all the larger cells are eventually resolved into broods of similar small ones, from which the embryo and its several parts are formed, Vogt believes that the peripheral and central cells are essentially different from each other, and are each destined to perform a separate part in the development of the embryo. The earliest formed cells of the periphery of the yolk, in the opinion of the latter observer, are employed to lay down the foundations of the embryo and of its principal organs, and in the immediate neighbourhood of each of these cells (but not within them), successive broods of new cells are subsequently developed to supply the wants of the growing parts: while the cells of the centre of the yolk, on the other hand, appear to have no other purpose than to elaborate fresh nutritive material or cytoblastema, out of which the above mentioned successive growth of new cells may be effected. As each of these large cells discharges its nutritive contents, it dissolves and disappears: being directly concerned neither in the formation of any part of the embryo, nor in the production of fresh broods of cells, and differing, therefore, in both these respects, from the cells of the peripheral part of the yolk. Another important point of difference in the opinions of Vogt and Reichert, as may be deduced from what has just been said, is that the latter considers the whole of the yolk to be directly concerned in the formation of the embryo and its several parts: while Vogt refers this formation entirely to the peripheral or cortical portion. In this view, Vogt is supported by several facts, especially by what he has observed in the development of the embryonic salmon; for, in the ova of these animals, the yolk, as before remarked, consists almost entirely of a homogeneous fluid substance in which there is no appearance of cells, except at the very surface, where alone the embryo is formed: the remainder of the yolk must, in this case, therefore, be regarded merely as a nutritive fluid.

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* Hist. Nat. des Poissons, t. i. p. 11.

According to Reichert's account of the development of the embryo frog,* it would seem that the first act of the process consists in the formation at the surface of the ovum of a fine membranous layer of cells, which, by extending over the whole surface, shortly constitutes a complete investment surrounding the yolk. And, in his opinion, it is not until this investing membrane is completely formed, that the development of the first formed parts of the embryo — namely, the two oval masses and the primitive groove between them—commences. From the observations of Vogt,† however, it appears that, in the development of the toad, no such investing membrane is formed. The earliest peripheral yolk-cells, it is true, unite together so as to form a kind of membrane at the surface of the yolk, but, as before observed, the primitive groove and laminæ dorsales are developed in the substance of this layer of cells and not beneath it. And it is only at a later period of the development of the embryo, that anything like an investing membrane is formed over its exterior, and this consists simply of a layer of pavement epithelium. A like absence of investing membrane was also observed by him in the ova of the salmon.‡ So that either Reichert's account must be considered erroneous, or, it must be concluded, that, in its earliest stages of development, the embryo pursues a different course in frogs, than in other amphibia and than in fishes.

Further information relating to the development of the several parts of the embryo of amphibia and fishes, is contained under the "Development of Organs."

The information we are in possession of, in relation to the changes ensuing in the ovum of *Mammalia* § at this stage, is derived almost exclusively from observations made by Bischoff upon the ova of rabbits and bitches. Some few of the facts to be here mentioned have been already stated in Müller's Physiology|| but it will be necessary to repeat them in order to preserve the continuity of the account.

About the time at which the mammiferous ovum reaches the uterus, the process of division and subdivision of the yolk appears to have ceased, its substance having been resolved into its ultimate and smallest divisions, while its surface presents a uniform finely-granular aspect,

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* Müller's Physiology, p. 1521.

† Entwickelungs-gesch. der Geburtshelferkröte, p. 32.

‡ Hist. Nat. des Poissons, t. i. p. 48.

§ Respecting the development of Birds no new facts of importance have recently been added to our knowledge. A series of plates illustrating the changes which the embryo of the chick undergoes during its development have been published by Prof. M. P. Erdl. (Entwickelung des Menschen und des Hünchens im Eie. 2. Bd. Leipsic, 1845.)

|| pp. 1560-64.

instead of its late mulberry-like appearance. The ovum indeed appears at first sight to have lost all trace of the cleaving process, and, with the exception of being paler and more translucent, almost exactly resembles the ovarian ovum; its yolk consisting, apparently, of a confused mass of finely granular substance.* But on more careful examination it is found that these granules are aggregated into numerous minute spherical masses, each of which contains a clear vesicle in its centre, but is not, at this period, provided with an enveloping membrane, and possesses none of the other characters of a cell.† The zona pellucida, and (in the rabbit) the layer of albuminous matter surrounding it, have at this time the same characters as when at the lower part of the Fallopian tube.

Shortly after this, important changes begin to ensue. Each of the several globular segments of the yolk becomes surrounded by a membrane, and is thus converted into a cell, the nucleus of which is formed by the central vesicle, the contents by the granular matter originally composing the globule; these granules usually arrange themselves concentrically around the nucleus.‡ When the peripheral cells, which are formed first, are fully developed, they arrange themselves at the surface of the yolk into a kind of membrane, and at the same time assume a pentagonal or hexagonal shape from mutual pressure, so as to resemble pavement epithelium. As the globular masses of the interior are gradually converted into cells, they also pass to the surface and accumulate there, thus increasing the thickness of the membrane already formed by the more superficial layer of cells, while the central part of the yolk remains filled only with a clear fluid. By this means the yolk is shortly converted into a kind of secondary vesicle, situated within the zona pellucida, and named by Bischoff, "vesicula blastodermica."§ The similarity of the several parts of this process with those observed by Vogt to take place in the ova of the frog (page 77) is very striking, and it is probable that the series of changes in the one are exactly analogous to those in the other. While these changes are proceeding within the yolk, which is at the same time gradually increasing in size, the zona pellucida and the layer of albuminous matter outside gradually coalesce, and so form a single membrane, the external investment of the ovum, from which the chorion is shortly afterwards produced.

In consequence of these changes, the Mammiferous ovum, when examined at this period, is found to consist of two nearly transparent vesicles enclosed one within the other, but differing from each other in composition.|| The external vesicle, which in the rabbit is formed, as above noticed, by the coalescence of the zona pellucida and albuminous covering,

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* Bischoff, Entwickelungs-geschichte des Kaninchen-eies, p. 85. † Op. cit. p. 86.

‡ Bischoff, op. cit. p. 92, and Entwick. des Hunde-eies, p. 65. § Op. cit. p. 90.

|| See the account given by Von Baer, Wagner, and others, who also describe the two coats of the ovum. Müller's Physiology, p. 1561.

in the bitch by the zona pellucida alone, is textureless, solid, but exceedingly fine and delicate. The internal vesicle, on the other hand, is formed, in the manner before described, of hexagonal cells; within each of which a nucleus is usually observed. This internal vesicle, or vesicula blastodermica, shortly after it is formed, undergoes a rapid increase in extent and thickness; its growth being effected apparently by the development of new cells. Concerning the mode in which these new cells are developed, however, Bischoff cannot speak with certainty, though having observed that while the growth of the vesicula blastodermica proceeds, the granules within the already formed cells gradually diminish in number, he thinks it not improbable that these granules are employed in the production of new cells, and that possibly each granule constitutes a nucleus, around which a fresh cell is developed;* but he has never witnessed anything resembling the development of one cell within another, and he considers it very questionable if this mode of multiplication is ever pursued in the yolk.

Very soon after its formation, the vesicula blastodermica presents at one point on its surface an opake roundish spot, which is produced by an accumulation of cells and nuclei of cells, of less transparency than elsewhere. This space, the "area germinativa" (Fruchthof), is the part at which the embryo first appears. It was supposed by Reichert,† that in the chick, and also in Mammalia, the appearance of this, the first trace of the embryo, was preceded by the formation, at the surface of the yolk, of an investing membrane, beneath which the area germinativa is formed, but Bischoff shews that certainly in Mammalia (as Vogt also shewed to be the case in amphibia and fishes, page 80), no such investing membrane exists, and that the area germinativa is formed upon the surface of the germinal membrane and covered only by the zona pellucida, or external membrane of the ovum as it has now become.‡

Bischoff has also found § that the germinal membrane of the Mammiferous ovum presently becomes divided into two distinct laminæ, in the same manner as has been long known to take place in the ova of birds.‖ This division is at first most manifest at the situation of the area germinativa, but it soon extends from this point and implicates nearly the whole of the germinal membrane. Bischoff has adopted for these laminæ the same names that are applied to them in the chick, namely, for the external one, the serous, or animal layer; for the internal one, the mucous, or vegetative layer. He has not been able to find the third layer described by Reichert as existing in the ova of the chick, and called by him membrana intermedia.¶

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* Entwickelungs-geschicte des Hunde-eies, p. 66.

† Müller's Physiology, p. 1543.

‡ Entwickelungs-geschichte des Hunde-eies. p. 68.

§ Entwickelungs-geschichte der Säugethiere und des Menschen. Leipsic, 1842, p. 59.

‖ Müller's Physiology, p. 1533.

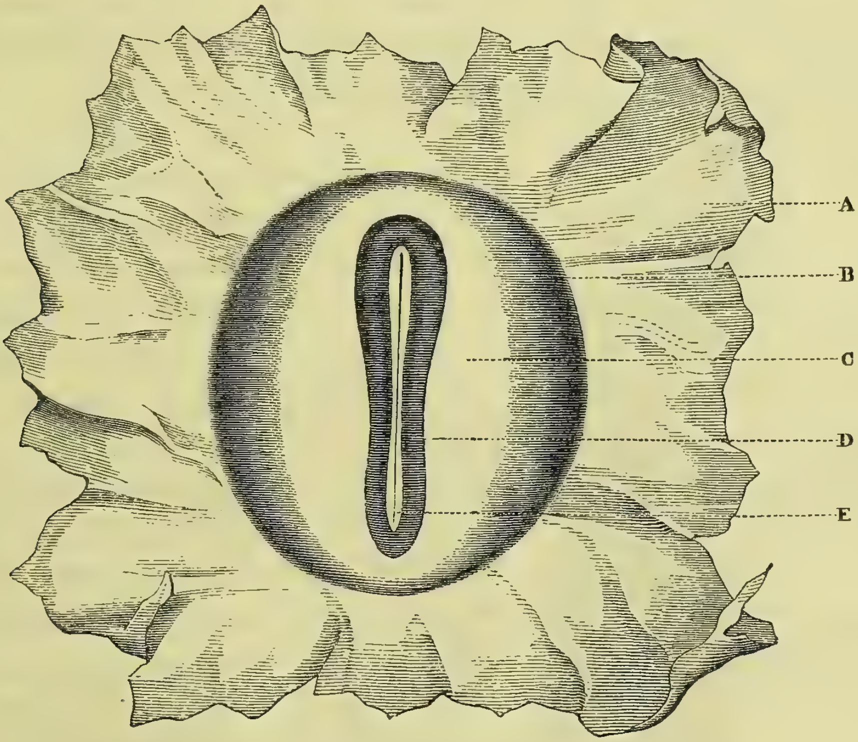
¶ Müller's Physiology, p 1544.

OF THE DEVELOPMENT OF THE EMBRYO.

1. *In Mammiferous Animals.*[*]

From the observations of recent embryologists, especially of Professor Bischoff,[†] it would appear that in the earlier periods of its formation the Mammalian embryo presents a close resemblance to the embryo of the chick, and that (as was shewn by Prévost and Dumas)[‡] the process of development in each takes place according to the same general plan. We have already traced the changes which ensue in the Mammiferous ovum subsequent to impregnation, as far as the formation of the area germinativa, and the separation of the germinal membrane into two layers. At its first appearance the area germinativa has a rounded form, but it soon loses this and becomes oval, then pear-shaped, and while this change in form is taking place, there gradually appears in its centre a clear space or area pellucida (fig. 10, C), bounded externally by a more opaque circle which subsequently becomes the area vasculosa (B). In the formation of these two spaces, both the serous and mucous laminæ of the germinal membrane take

Fig. 10.[§]



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[*] Chapter iii. p. 1560 of Müller's Physiology.

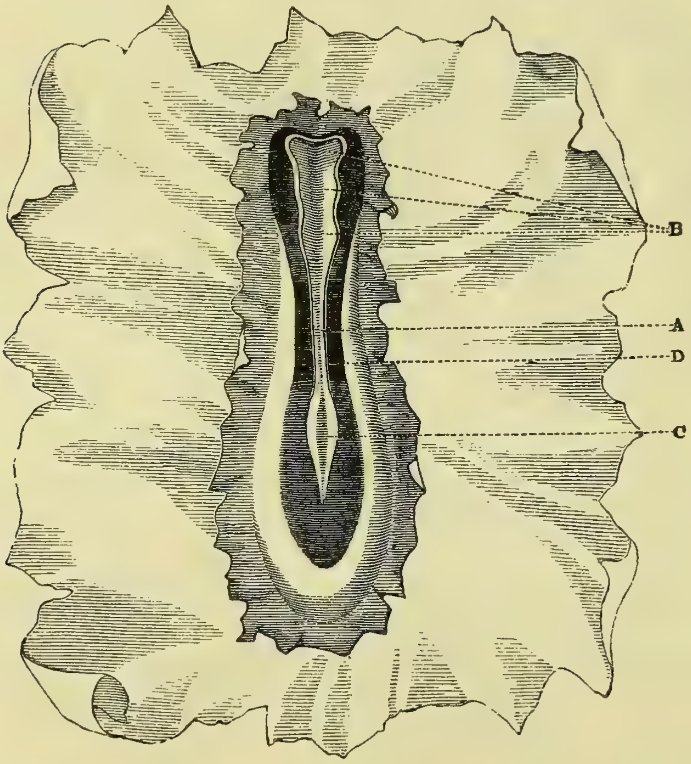
[†] Operibus citatis.

[‡] Müller's Physiology, p. 1566.

[§] Fig. 10. Portion of the germinal membrane of a bitch's ovum, with the area pellucida and rudiments of the embryo; magnified ten diameters. A. Germinal membrane. B. Area vasculosa. C. Area pellucida. D. Laminæ dorsales. E. Primitive groove, bounded laterally by the pale pellucid substance of which the central nervous system is composed. After Bischoff. (Entwickelungs-geschichte des Hunde-eies.)

part. The comparative obscurity of the outer space—the area vasculosa—is due to the greater accumulation of nucleated cells and nuclei at that part than in the area pellucida. The first trace of the embryo in the centre of the area pellucida, consists, not of a projecting line, as described by Von Baer, but of a shallow groove (E), as shewn especially by Reichert in the embryo of the chick.[*] This is formed in the external or serous fold alone of the germinal membrane: the mucous fold having no direct share in its production. Coincidently with the formation of the primitive groove, two oval masses, the laminæ dorsales (D) appear, one on each side of the groove. Their form changes according as does that of the area pellucida: passing gradually with the latter from an oval to a pyriform shape, and eventually becoming guitar-shaped. The upper borders of these two masses gradually tend towards each other, as in the embryo of the chick, and ultimately unite, so as to convert the primitive groove into a canal or tube. But with regard to the mode in which these masses unite, and to their own nature, and the changes which ensue in them, Bischoff maintains a different view to that advocated by Reichert. The latter physiologist supposed that, at least in the chick and in the frog, these oval masses constitute the rudimentary parts of the central nervous system, but Bischoff is of opinion with Von Baer, that in Mammalia they are the foundations of the dorsal part of the trunk of the embryo, while the nervous system is developed, as will be hereafter more fully described, only from their most internal part, that, namely, which forms the bottom and sides of the primitive groove. Shortly after, or, as shewn in fig. 11 from a bitch's ovum, even before the laminæ dorsales have closed over the primitive groove, a few square-shaped, at first indistinct, plates, which are the rudiments of vertebræ (fig. 11, D), begin to appear at about the middle of each. It is not possible to perceive at this time the chorda dorsalis so distinctly observed in birds and fish; but later, when the bodies of the

Fig. 11.[†]



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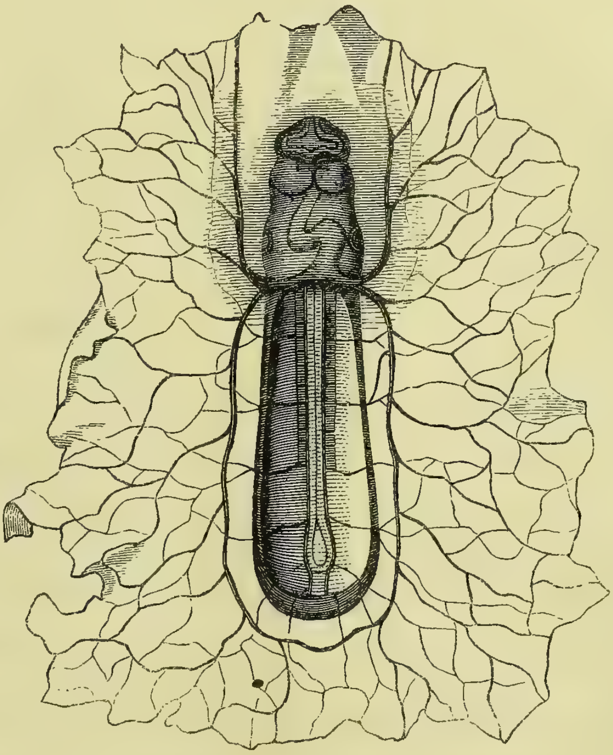
[*] Müller's Physiology, p. 1547.

[†] Fig. 11. Portion of the germinal membrane, with rudiments of the embryo from the ovum of a bitch. The primitive groove, A, is not yet closed, and at its upper or cephalic

vertebræ have begun to be formed, an appearance of a chorda in their centre is perceptible. The two laminæ viscerales or ventrales, which, as described by Von Baer, are also formed in the serous fold, and proceed from the laminæ dorsales, continue at first on the same plane with the germinal membrane, and only by degrees bend downwards and inwards towards the cavity of the yolk, where they unite and form the anterior walls of the trunk. While the borders of the primitive groove are approaching each other and about to close, the groove itself at its anterior extremity dilates into three recesses or vesicles (fig. 11, B), which, with the nervous matter developed in them, constitute the rudimentary brain; at the same time, the surrounding parts assume the characters of the head of the embryo which raises itself above the surface and bends forwards and downwards as in the chick. During the development of the above parts of the embryo, an accumulation of cells takes place between the two laminæ of the germinal membrane at the area vasculosa. These cells shortly form themselves, as in the bird, into a distinct layer—the vascular lamina—which serves as a groundwork in which the first blood-vessels of the embryo are developed. The mode in which this development of vessels takes place will be described hereafter.

Fig. 12.*



Amnion.—The development of the amnion, which, as was pointed out by Von Baer, is effected in Mammalia just as in birds, takes place very rapidly, being completed by the end of twenty-four hours after the first appearance of the primitive groove.†

Umbilical vesicle. — Having remarked on the existence of an umbilical

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end presents three dilatations, B, which correspond to the three divisions or vesicles of the brain. At its lower extremity the groove presents a lancet-shaped dilatation (sinus rhomboidalis) C. The margins of the groove consist of clear pellucid nerve-substance. Along the bottom of the groove is observed a faint streak, which is probably the chorda dorsalis. D. Vertebral plates. After Bischoff. (Ibid.)

* Fig. 12. Embryo from a bitch at the 23d or 24th day, magnified ten diameters. It shews the net-work of blood-vessels in the vascular lamina of the germinal membrane and the trunks of the omphalo-mesenteric veins entering the lower part of the S-shaped heart. The first part of the aorta is also seen. After Bischoff. (Ibid.)

† Bischoff, Entwick. der Säugeth. und des Menschen, p. 108.

vesicle in the embryos of all Mammalia yet examined, on its being invariably situated on the outside of the body of the embryo, and on its disappearance in all, either before, or at the termination of intra-uterine life, Bischoff [*] confirms the observations of Von Baer and Coste,[†] that in its ulterior relations to the embryo this vesicle presents considerable varieties in the different classes of Mammalia. In ruminants and pachyderms, although at its first formation the umbilical vesicle grows with extreme rapidity, yet very shortly its development is arrested, and it then begins to disappear. In the embryos of cows not more than six lines long, the middle portion alone is found still in existence, and its attachment to the intestine consists no longer of a canal, but only of a thread-like pedicle. Its blood-vessels also have undergone a proportionate reduction. In the pig an almost equally early disappearance of the vesicle is observed. In Carnivora, on the contrary, the umbilical vesicle remains during the whole period of intra-uterine existence; presenting itself as a cylindrical sac, the surface of which is throughout abundantly supplied with omphalo-mesenteric vessels, and the cavity of which is long in direct communication with that of the intestine. The left side of the vesicle is covered by the allantois, while its right side is in contact with the chorion. At a certain period the vesicle surrounds the upper part of the embryo in such a manner that this part appears as if contained within its cavity, and has been so described by some embryologists. But at a later period when the embryo has detached itself from this relation to the vesicle, the error of such a supposition is rendered manifest. In rodents, the rabbit for example, the umbilical vesicle also persists during the whole of intra-uterine life, and at one period there is observed a similar deceptive appearance as in Carnivora, of the embryo being contained within the cavity of the vesicle.

Allantois.—According to Bischoff,[‡] the allantois of the Mammalian embryo is developed neither from the intestinal tube, as stated by Von Baer, Rathke, Valentin, and others, nor from the Wolffian bodies, as was said by Reichert,[§] to be the case in the chick; for at the time of its first appearance no trace either of the intestinal canal or of the Wolffian bodies can be perceived. At its earliest appearance, the allantois in the rabbit consists of a solid mass of cells projecting from the visceral plate of the tail. But in the dog this mass is at first double (figs. 13 and 14), though the two halves soon fuse together, and are converted into a single vesicle. The allantois is abundantly vascular, for it contains the ramifying extremities of the two arteries which run along the sides of the vertebral arches, and of the two veins which are situated within the walls of the visceral laminæ. These vessels subsequently become the umbilical arteries and veins. When the allantois has assumed the form of a vesicle, it then communicates both with the intestinal tube and the corpora Wolffiana, though the mode in which this communication is effected is not quite clear. The allantois now rapidly increases in size, and the two umbilical arteries in connection with it are recognised as branches of the iliac, while the umbilical veins unite into either one or two trunks, which empty themselves in the liver and the inferior vena cava. As the visceral laminæ close in the abdominal cavity, the allantois is thereby divided at the umbilicus into two portions, the smaller of which is retained in the abdomen, and is converted into the urinary bladder, while the external and larger portion, accompanied by the umbilical vessels, proceeds to the chorion, where its vessels are brought into connection with those developed within the villi of this structure. The middle portion of the allantois, that, namely, which traverses the umbilicus, at first contracts into a canal, and subsequently is converted into a fibrous cord, the urachus.‡ The different modes in which the allantois is subsequently disposed of in the different orders of Mammalia, are described by Bischoff almost as they were by Von Baer,§ whose account Bischoff for the most part confirms.

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[*] Op. cit. p. 113.

[†] Müller's Physiology, p. 1570.

[‡] Entwick. der Säugeth. und des Menschen, p. 116; and Entwick. des Kaninchen-eies, p. 122.

[§] Müller's Physiology, p. 1554.

Fig. 13.*

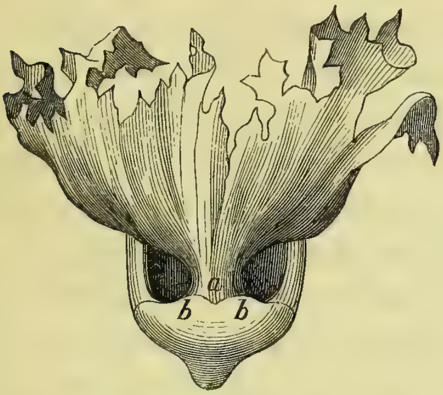
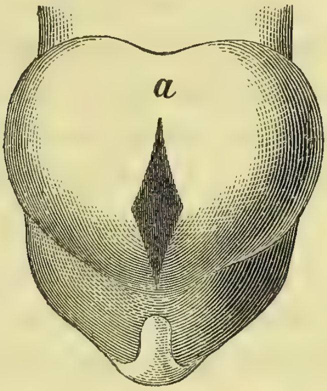


Fig. 14.†



The development of the other parts of the Mammalian embryo will be considered under the "Development of Organs," for, to avoid repetition, it is deemed advisable to combine in one general account all the new information on this subject, which has been obtained from observations on different classes of animals.

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* Fig. 13. The lower part of the body of a bitch's embryo, magnified 10 diameters. The mucous and vascular layers of the germinal membrane are turned back to shew (*a*) the pedicle of the umbilical vesicle at its entrance into the abdominal cavity. *b. b.* Two cellular masses out of which the allantois is formed. After Bischoff.

† Fig. 14. The lower extremity of an older embryo. The allantois *a* is developed into a single vesicle, but its origin from two symmetrical halves is still shewn, especially by the fissure in the middle. (Ibid.)

‡ See Langenbeck's Account of the Allantois in the Human Ovum, on the next page.

§ Müller's Physiology, p. 1570.

2. *In the human subject.*[*]

Allantois.—Bischoff[†] inclines to the same view of the development and office of the allantois of the human embryo, as was maintained by Professor Müller[‡] and many other embryologists, namely, that, as is the case in the embryo of rodent animals, it is developed merely as a narrow vesicle which elongates itself till it reaches the chorion, and is only destined to conduct the umbilical vessels to that structure, having done which, it disappears, the urachus of the urinary bladder being its only remains. In further refutation of the opinion of Velpeau and other anatomists who consider that after its formation, the allantois increases rapidly, and as in ruminants, surrounds the embryo together with its amnion and umbilical vesicle, uniting by one of its layers with the chorion, by the other with the amnion, Bischoff draws attention to three principal circumstances which are opposed to this view. First, no one has yet observed the smallest trace of the allantois, either on the internal surface of the chorion, or on the external surface of the amnion; both the chorion and amnion are perfectly simple membranes. Secondly, in all cases in which the allantois applies itself upon the other membranes of the embryo, it furnishes these with vessels, so that in pachyderms, ruminants, and Carnivora in which the allantois is thus disposed, the chorion and amnion are at a certain period, richly supplied with vessels; but in the human ovum nothing like this occurs, no vessels at any period of its existence are ever found in either of these membranes, except at that part where the allantois comes into contact with the chorion and at which the placenta is subsequently developed. Thirdly, if, as assumed, the allantois in its development passes at all parts between the chorion and amnion, it must necessarily invest the umbilical vesicle, on one side or the other; but this is never found to be the case.

So far as concerns the refutation of Velpeau's hypothesis, the account of the human allantois recently published by Dr. Max Langenbeck[§] accords with that of Bischoff. But Langenbeck has proceeded further and has given a more satisfactory explanation of the probable nature and ultimate condition of this structure than has been afforded by any previous physiologist. His researches shew that the allantois at an early period comes into immediate relation with the Wolffian bodies—in this agreeing with Reichert in his observations on the chick[||] and, moreover, is concerned more directly, and in a different manner than has yet been described, in the formation of the urinary bladder. At its first development the allantois of the human embryo appears, as has been described by others, in the form of a somewhat pear-shaped body protruding from the pelvic portion of the trunk, and soon becomes vesicular. Shortly after its formation there is observed a narrowing of that portion of the vesicular body nearest the fœtus, (fig. 15, 3) while the more distant portion undergoes a rapid increase in size, and gradually approaches the chorion, to which structure the numerous vessels surrounding the allantois are thus conducted from the body of the fœtus. This object attained, the development of the allantois is completed, and the subsequent changes which it undergoes appear to be retrograde ones. The first of these changes which ensues is the production of a kind of twist or constriction on that side of the vesicular part of the allantois turned towards the chorion (fig. 15, 7); this is the commencement of the formation of the urachus. The vesicular part constitutes the rudiment of the urinary bladder, and maintains its connection with the body of the embryo by means of the narrowed tubular part (3) already alluded to (and which has been hitherto, but erroneously, described as the urachus). This tubular part, indeed, forms a direct communication between the urinary bladder and the primordial kidneys or Wolffian bodies, by dividing into two portions, each of which passes directly into the corresponding Wolffian body, and thus the ureters are formed.† As the embryo increases in size, and the Wolffian bodies gradually disappear to be replaced by the kidneys, the ureters together with the urinary bladder—which by degrees loses its round or elliptical form to be elongated in the direction corresponding to the length of the umbilical cord—are drawn into the cavity of the pelvis. When this has occurred the bladder assumes a club-shaped form, the base of which represents the fundus of the organ, while the apex tapers upwards to pass into the urachus, which for some little distance is therefore tubular. Langenbeck cannot speak with certainty respecting the length of time required for the bladder to be thus drawn into the body of the embryo; but he considers that by the twentieth week the process is always completed, frequently even by the twelfth. For long after this period, however, the

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[*] Müller's Physiology, p. 1572.

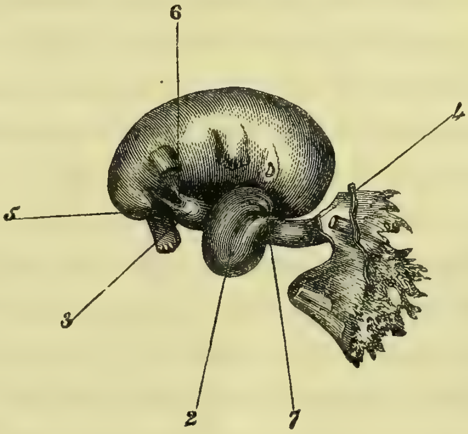
[†] Entwick. der Säugeth. und des Menschen, p. 129.

[‡] Physiology, p. 1582.

[§] Untersuchungen über die Allantois. Göttingen, 1847.

[||] Müller's Physiology, p. 1554.

Fig. 15.*



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* Fig. 15. Human fœtus with the umbilical cord, allantois, and a portion of the chorion. After Langenbeck. The right hind extremity has been removed. 2. Allantois (or rudiment of the urinary bladder). 3 and 4. Umbilical cord. 5. Ureters. 6. Ductus vitello-intestinalis. 7. Fold or constriction of the allantois, indicating the first formation of the urachus.

† This division and the junction of the branches with the extremities of the Wolffian bodies, has been observed also by Professor Budge in a five-weeks old human embryo. (Müller's Archiv. 1847, p. 9.)

portion of the urachus between the bladder and the umbilicus remains tubular, and in some instances it continues permanently in that condition, so that urine can escape from the umbilicus.*

Amnion.—M. Serres† has again maintained that the amnion of the human embryo, instead of being produced by a fold of the external layer of the germinal membrane rising up and gradually enveloping the embryo, is originally an independent vesicle outside the embryo, and that the latter connects itself with it by dipping into, and eventually completely enveloping itself with it. This view has been supported also by MM. Maignien and Jacquart,‡ from the appearances presented by an early aborted embryo; but from Bischoff's§ account it would seem that both these observers as well as M. Serres must, in the specimens examined by them, have overlooked the true amnion, which from the early age of the embryos or from some morbid change may have been obscured, and probably mistook for it either the allantois or the umbilical vesicle. In his work on embryology,‖ Bischoff states the various arguments in favour of the view that the amnion of the human ovum observes the same mode of development as obtains in other Mammifera.

Chorion.—Little requires to be said of the chorion of the human ovum. It does not appear to present any essential difference from the chorion of other Mammalia. Its formation around the ovum in rabbits and bitches has been already described. In the former animals it is developed apparently from the zona pellucida and the layer of albuminous matter by which the zona is surrounded; but in the bitch, in which no such albuminous deposit occurs, it is developed (according to Bischoff) from the zona pellucida alone. Bischoff believes that the human ovum, like that of the bitch, is unprovided with an albuminous covering, and that the chorion in this case also is formed directly from the zona pellucida; but Mr. Wharton Jones is inclined to doubt this statement. The villi of the chorion, as stated elsewhere, are, at their first appearance, composed entirely of cells, and it is not until the arrival of the allantois at the chorion, that vessels are developed within them.

Formation and structure of the decidua..—The subject of the formation and structure of the membrana decidua, has within the last few years been investigated anew by several physiologists, and the general tendency of the results obtained by them is to confirm the opinion of Dr. Sharpey and of Prof. E. H. Weber, stated at page 1574 of Müller's Physiology, that this membrane is not a structure of new formation, but is produced simply by an increased development of the parts composing the mucous membrane of the uterus, and of an increased quantity of matter secreted by the follicles of this membrane. In further support of this opinion, E. H. Weber* has contributed some additional particulars relating to the mode of formation of the decidua, and the ultimate destination of its several parts. They do not, however, throw much further light on the subject than was already afforded by the researches of Dr. Sharpey. Many of the observations of the latter physiologist, Weber amply confirms. He corroborates, for example, all that was stated by Dr. Sharpey concerning the existence and peculiarities of the two sets of glands found in the mucous membrane of the bitch's uterus, and of the changes which ensue in these glands after conception. The only point in which, on this subject, Weber's account differs from that of Dr. Sharpey, is in describing the vascular processes of the chorion as sending off their branches within the glands of the mucous membrane of the uterus, and carrying the lining membrane of the glands with them in folds which they form around the maternal vessels, whereas Dr. Sharpey states that the fœtal processes send off their branches outside the uterine glands, and describes the expanded summits of these processes which close the mouths of the glands, as being "smooth and even, and covered with a prolongation of the same epithelium which lines the cells" —or dilated parts of the glands. Dr. Sharpey also describes these glands as remaining during pregnancy, and secreting a fluid which is probably absorbed by the fœtal vessels as nutriment for the fœtus; but, according to Weber's account, these glands, or, at least, the dilated or cell-like portions of them, entirely disappears as the fœtal blood-vessels come into relation with those of the mother. Professor Weber confirms Dr. Sharpey's description of the simple follicles observed on the mucous membrane of the human uterus immediately after impregnation. He could never observe that these follicles formed dilated pouches previous to opening upon the surface of the uterus, as in the bitch, or that at their opposite extremity they branched or even divided into two trunks; but he noticed that at their termination in the substance of the uterus, they frequently formed two or three closed sacculi. (See fig. 16, p. 92.) He states that he could never perceive the villi of the chorion to enter the orifices of these glands, although Bischoff† (whose account of the uterine glands and of the membrana decidua, in other respects corresponds closely with the descriptions given by Dr. Sharpey and Professor Weber) considers it probable that they do. The existence of these simple glands in the mucous membrane of the unimpregnated human uterus, appears to have never yet been clearly demonstrated, although their appearance immediately after impregnation and the existence of them in the unimpregnated uterus of the bitch, and many other animals, renders it highly probable that in the human uterus also they exist previous to impregnation, although of such minute size that they have hitherto escaped detection.

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* An account of the early development of the allantois of the human ovum is furnished by M. Serres (An. des Sc. Nat. 1843; and Gazette Med. de Paris, 1843, p. 414), but it contains nothing essentially new. Serres is of the same opinion with Langenbeck concerning the close relation subsisting between the allantois and the corpora Wolffiana. For Coste's view of the human allantois, *vide* Gaz. Med. 1843, p. 696; and for that of Velpeau and others, see the account in the same journal of the discussion which ensued among the members of the Academy of Sciences, after the reading of M. Serres's memoir.

† Gazette Médicale, Juin, 1843.

‡ Gaz. Med. Novembre, 1843.

§ Müller's Archiv. 1844, Jahresbericht, p. 144.

‖ Op. cit. p. 132 *et seq.*

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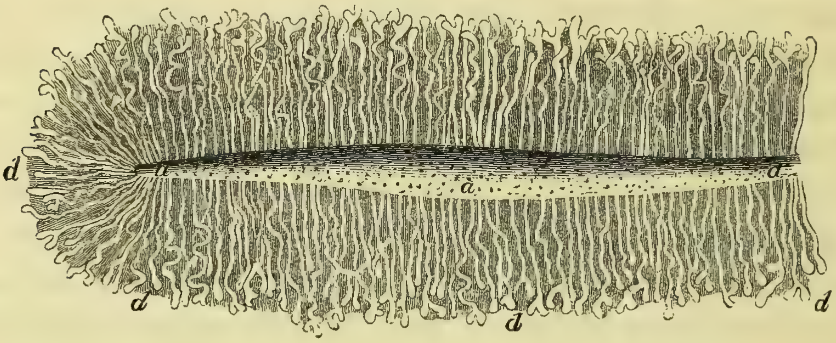
* Zusätze zur Lehre vom Baue und den Verrichtungen der Geschlechtsorgane. Leipzig, 1846.

† Müller's Archiv. 1846, p. 112.

Fig. 16.*



According to the account furnished by Weber, and that given by the other physiologists who have written on the subject, the mucous membrane of the uterus immediately after conception becomes swollen and soft, the cilia of its epithelial cells disappear (Weber),† its tubular glands and the vascular network occupying the spaces between them increase considerably in size, whilst, as shewn both by Professor Weber and Professor Goodsir,‡ a substance composed of nucleated cells fills up the inter-follicular spaces in which the bloodvessels are contained. To this inter-follicular substance Professor Goodsir attributes much of the increased thickness of the mucous membrane, and he considers that it plays an important part in the further purposes of the decidua. When thus developed, the mucous membrane of the uterus, according to Professor Goodsir, begins to secrete largely, and the cavity of the uterus is shortly filled with the secreted fluid which constitutes the "hydroperione" of Breschet. The portion of this secretion by which the os uteri is plugged up, is composed of elongated epithelial cells; whilst the portion which immediately surrounds the ovum consists of cells of a spherical form. To these latter cells Professor Goodsir attributes an important office, that, namely, of preparing nutritive material for the ovum by their further development and the production of successive quantities of new cells.

It is of these cells also, according to the same observer, that the decidua reflexa is formed, and not, as was formerly supposed, by the ovum protruding into and carrying before it a portion of the decidua vera on its entrance into the uterus. But E. H. Weber * is of opinion that the decidua reflexa is really formed of a layer or reflection of the decidua vera, and he considers his opinion to be supported by the fact, that in very small ova, minute openings, apparently of the uterine follicles, are found not merely at the margins next the decidua vera (to which situation they were observed by Dr. Sharpey to be chiefly, though not entirely, confined),† but also extend as far as the middle of the decidua reflexa. He found these openings quite distinct even in an embryo examined at the commencement of the third month of pregnancy. In the formation of this reflected portion of the decidua, he believes that the ovum on its entrance into the uterus, is either received into a fold of the thickened mucous membrane (or decidua vera), which at this part—which may be situated at the junction of the Fallopian tube to the uterus, or in the anterior or posterior wall of this organ—is more developed than elsewhere, and that as it enlarges it carries along with it a covering of this membrane in the manner suggested by Dr. Sharpey; ‡ or that it becomes simply invested by a superficial layer of the decidua vera, which at the point where the ovum comes in contact with it, separates from the deeper portion and carries with it apertures corresponding to the orifices of the uterine glands—just as cuticle raised by a blister bears with it the openings of the sudoriferous ducts. A view somewhat similar to the first of these appears to be entertained also by M. Coste.§

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* Fig. 16. Section of the lining membrane of a human uterus at the period of commencing pregnancy, shewing the arrangement and other peculiarities of the glands *d. d. d.*, with their orifices, *a. a. a.*, on the internal surface of the organ. Twice the natural size. After E. H. Weber.

† Froriep's N. Notizen, No. 507, p. 1, 1842.

‡ Anatomical and Pathological Observations, Edinburgh, 1845.

Formation and Structure of the Human Placenta.||

A very complete account of the structure of the human placenta, has been given by Professor Goodsir:¶ his paper has been already referred to, but it now requires a more detailed notice. In many respects his description agrees with that furnished by Professor Weber, Dr. Reid, and Mr. Dalrymple, as contained in Müller's Physiology.** The existence of two distinct portions in the placenta, the one belonging to the fœtus and the other to the parent, is clearly shewn, and he finds that the communication between these two portions is effected by means of nucleated cells.

As already stated, Professor Goodsir considers the decidua reflexa to be formed of a number of cells secreted by the enlarged follicles of the mucous membrane of the uterus; that these cells possess the power of further development and of multiplication; and that eventually they completely surround the chorion, to the absorbing villi of which they supply nutritive material for the embryo. At the earliest period of

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* Op. cit. p. 35.

† Müller's Physiology, p. 1580.

‡ Müller's Physiology, p. 1580.

§ Comptes Rendus, 24 Mai, 1847, p. 893.

|| Müller's Physiology, chapter iv. p. 1604.

¶ Op. cit. p. 50.

** P. 1604, *et seq.*

their formation the villi of the chorion consist of nucleated cells, bounded externally by a fine transparent membrane, and are immersed in the substance of the cellular decidua reflexa, from which they absorb nutriment for the embryo. When, however, the embryo has attained a certain stage of development, at which the allantois containing the umbilical vessels arrives at the internal surface of the chorion, and at which blood-vessels are also formed within the villi * and communicate with the umbilical vessels, the villi at that part which is to be converted into the placenta, increase in number and in size, and come into relation with the vascular system of the mother. At this period each villus contains one or more loops of blood-vessels, its cells are diminished in quantity, but a few are always found at its terminal extremity, and it still possesses its external investing membrane. Meanwhile the vessels of the decidua vera, or highly-developed mucous membrane of the uterus, enlarge, and "assume the appearance of sinuses encroaching on the space formerly occupied by the cellular decidua, in the midst of which the villi of the chorion are imbedded. This increase in the calibre of the decidual capillaries goes on to such an extent that finally the villi are completely bound up or covered by the membrane which constitutes the walls of the vessels, this membrane following the contours of all the villi, and even passing to a certain extent over the branches and stems of the tufts." In this manner, as was shewn by Dr. J. Reid, Weber, and other observers,† the tufts and villi of the fœtal portion of the placenta are completely ensheathed by the lining membrane of the vascular system of the mother. Between this membrane of the enlarged maternal vessels, and the membrane of each villus, there still remains a layer of nucleated cells of the decidua, (fig. 17 *b*), which the enlarging vessels have carried before them. These cells, at certain parts of the circumference of the villus, are grouped together in greater quantities, and appear to be passing off from a spot in the centre of the mass (*c*); each such group constitutes what Professor Goodsir calls a germinal spot, or nutritive centre, whose office appears to be to supply a constant succession of new cells in the place of those which are rapidly disappearing in the performance of the functions of the villus.

It appears, therefore, that, at the villi of the placental tufts, where the fœtal and maternal portions of the placenta are brought into close relation with each other, the blood in the vessels of the mother is separated from that in the vessels of the fœtus by the intervention of two distinct sets of nucleated cells, one of which belongs to the maternal portion of the placenta, is placed between the membrane of the villus and that of the vascular system of the mother, and is probably designed to separate from the blood of the parent the materials destined for the blood of the fœtus, while the other belongs to the fœtal portion of the placenta, is situated between the membrane of the villus and the loop of vessels contained within, and probably serves for the absorption of the material secreted by the other set of cells, and for its conveyance into the blood-vessels of the fœtus. In describing these several membranes and layers of cells as composing each placental villus, Professor Goodsir calls the lining membrane of the vascular system of the mother the external membrane of the villus (fig. 17 *a*), the layer of cells between this and the villus, the external cells of the villus (*b*), the membrane within these, the internal membrane of the villus (*e*), and the cells between this and the loop of vessels, the internal cells of the villus (*f*). Between the two sets of cells with their investing membrane there exists a space (*d*,) into which it is probable that the materials secreted by the external cells of the villus are poured, in order that they may be absorbed by the internal cells, and thus conveyed into the fœtal vessels. As the decidual vessels enlarge and extend themselves, so as to ensheath the placental tufts, their lining membrane forms numerous folds, the venous reflections of Dr. Reid, which pass from tuft to tuft, and villus to villus, connecting them together in the same manner as the intestines are tied together and held down in various places by reflections of the peritoneum. These folds or processes of the venous membrane appear in the form of innumerable threads passing from the sides or apex of one villus to that of another throughout the substance of the placenta. On minute examination, Professor Goodsir found that these threads were tubular, and that the membrane of which they were formed was distinctly continuous in one direction with the lining membrane of the enlarged decidual vessels, and in the other with the external membrane of the placental villi, forming, therefore, in this way, the central containing membrane of the bag of the placenta. The tubular portion of the threads was filled with cells, which were continuous in one direction with the cells of the placental decidua, in the other with the external cells of the villi. (See fig. 18, p. 96.)

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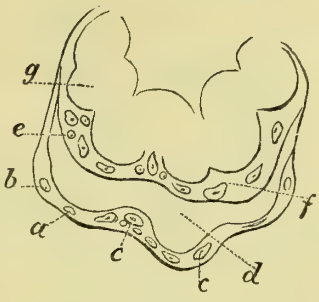
* This formation of blood-vessels within the villi appears to take place quite independently of any communication with the vessels of the embyro, with which they only subsequently unite (Bischoff, Entwick. der Säugeth. und des Menschen, p. 127); it is probably effected through the transformation of the cells of the villi, in a manner which will be pointed out hereafter when speaking of the mode of development of blood-vessels generally.

† Müller's Physiology, p. 1606. See also Weber's Zusätze der Geschlechtsorgane, p. 41.

Fig. 17.*



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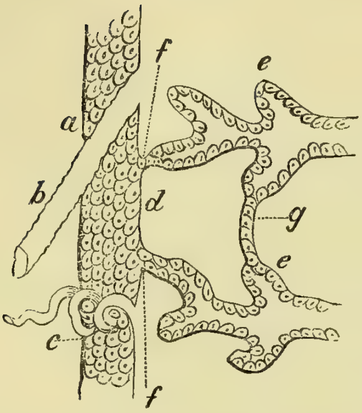
* Fig. 17. Extremity of a placental villus. *a*. External membrane of the villus, or lining membrane of the vascular system of the mother. *b*. External cells of the villus. *c c*. Germinal spots or centres of the external cells. *d*. Space between the maternal and fœtal portions of the villus. *e*. Internal membrane of the villus, or external membrane of the chorion. *f*. Internal cells of the villus, or cells of the chorion. *g*. Loop of umbilical vessels. After Goodsir.

Several varieties as to the mode of arrangement of the tuft of umbilical vessels in the villi are described by Professor Goodsir. The general rule is that one umbilical vessel enters a villus, forms a simple, more or less open loop, and passes out again without dividing. Occasionally the vessel divides, and its branches either pass out separate or anastomose into a single trunk again. Sometimes more than one vessel enters a single villus, which either divide into other branches, or leave the villus as they entered. Professor Goodsir confirms the fact observed by Professor Weber and Mr. Dalrymple,[†] that the same vessel may enter and retire from two or more villi before it becomes continuous with a vein.

Fig. 18.[*]



OF THE DEVELOPMENT OF ORGANS.[‡]

Development of the vertebral column and cranium.[§]

Chorda dorsalis.—A very minute account of the structure of the chorda dorsalis in Amphibia and fishes, and of the metamorphoses undergone by it, and by the surrounding cellular substance, in the formation of the several parts of the vertebral system, has been furnished by Vogt,[||] from observations made principally on the toad (Alytes obstetricans) on Tritons, and on the salmon (Coregonus palæa). In the former of these animals he observed, that at its earliest formation the chorda dorsalis contains no cells, being composed of a clear gelatinous-looking substance, with which are mingled, without any definite arrangement, numerous molecular bodies and a few plates of stearine. Shortly, numerous scattered roundish cells appear, consisting of a fine membrane, enclosing a pellucid gelatinous-looking fluid, and unprovided with a nucleus. They are formed at first at the cephalic extremity of the chorda, but soon multiply so rapidly, that in a short time the substance of the chorda is composed almost entirely of them, the granular matter being reduced to a small quantity of intercellular substance. As the cells increase in size, clear, flat, vesicular nuclei are shortly developed within them; they are sometimes central, sometimes parietal, never granular, or provided with a nucleolus. Around the cellular substance of the chorda, a closely fitting sheath is early developed; it appears first in the form of a clear pellucid fluid, but subsequently assumes a fibrous character, probably from the transformation of cells which are shortly developed in it. In the chorda of the Triton Lobatus, a granular substance similar to that in the chorda of the toad, is first observed; but instead of being scattered irregularly, the granules have a somewhat circular arrangement, being disposed like so many rings around the chorda. As in the toad, so also in the triton, these granules shortly disappear, and are replaced by cells, the formation of which presents itself first at the cephalic extremity, and rapidly extends through the whole length of the chorda. Like the granules which preceded them, these cells in the triton observe an orderly arrangement; each cell having a size equal to the diameter of the chorda, and, being flattened by the pressure of the adjoining cells, contributes in giving to the chorda the appearance of being composed of a linear series of rings enclosed within its fibrous sheath. The cells lie close to each other, very little intercellular substance being present. At a later period of the larval life of the triton, this regular arrangement of the cells is somewhat modified. The diameter of many parts of the chorda, instead of being occupied by only one nucleated cell, now presents two or three of about equal size.

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[*] Fig. 18. "A diagram illustrating the arrangement of the placental decidua. *a.* Parietal decidua. *b.* A venous sinus passing obliquely through it by a valvular opening. *c.* A curling artery passing in the same direction. *d.* The lining membrane of the maternal vascular system (external membrane of villus) passing in from the artery and vein lining the bag of the placenta and covering (*e e*) the fœtal tufts, passing on to the latter by two routes, first by their stems from the fœtal side of the cavity, secondly by the terminal and decidual bars (*f f*) from the uterine side, and from one tuft to the other by the lateral bar (*g*)." Throughout its whole course, except along the stems of the tuft, and the fœtal side of the placenta, this membrane is in contact with decidual cells. After Goodsir.

[†] Müller's Physiology, p. 1605.

[‡] Section iii. chap i. p. 1609 of Müller's Physiology. [§] Page 1610.

[||] Entwick. der Geburtshelferkröte, pp. 41 *et seq.;* and Histoire Naturelle des Poissons d'eau douce, by M. Agassiz, t. i.: works already quoted from.

Concerning the origin of the finely granular material of which the chorda is at first composed, and from which the cells are developed, Vogt is of opinion that it is furnished by embryonic cells. He considers that along the line to be subsequently occupied by the chorda dorsalis, are deposited embryonic cells similar to those from which all other organs of the embryo are formed: that the membranous walls of these cells shortly disappear, and that the cell contents thereby liberated constitute the granular matrix or cytoblastema from which the second set of cells of the chorda are formed.* Kölliker,† however, appears to be of opinion that the cells of the chorda dorsalis are produced directly from the primary embryonic cells which simply enlarge, and at the same time lose the granular matter which they originally contained. According to Prevost and Lebert,‡ again, they are formed from the enlarging nuclei of the embryonic cells. The development of the chorda dorsalis in the embryo of the salmon (Coregonus palœa) was found by Vogt * to pursue an almost similar course to that observed in the toad and triton. Very large cells are early observed in the position occupied by the chorda; these shortly disappear, leaving a transparent, faintly granular substance, from which the subsequent cells of the chorda appear to be produced.

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* This is in accordance with his opinion, again to be mentioned, that none of the embryonic tissues are developed directly from the first embryonic cells, but that these cells invariably resolve themselves into a secondary blastema, out of which are formed new cells, which give rise to the tissues of the embryo.

† An. des Sc. Nat. 1846, p. 92.

‡ An. des Sc. Nat. 1844, p. 206.

Vertebral column.—The nature of the changes undergone by the fibrous sheath of the chorda dorsalis of Alytes obstetricans, by which the development of the bodies of the vertebræ is effected, has also been minutely investigated by Vogt. In the first "laying down" of the individual segments of the vertebral column, the sheath of the chorda dorsalis can exercise no share, for, at the period at which this occurs, the sheath is not yet formed from that part of the substance of the chorda to which it owes its origin. From the time of its first appearance, however, the sheath becomes so intimately connected with the mass of cell-substance surrounding it, that it can at no time be completely separated therefrom. The first trace of solidification of the divisions of the vertebral column is observed immediately external to the sheath of the chorda: and presents itself in the form of cartilaginous rings adherent internally to the sheath, and externally to the surrounding cell-substance, which gradually assumes the characters of muscular tissue. At first, the lines of separation between the muscular, cartilaginous and fibrous layers of which the vertebral system is at this time composed, are very obscure; but, shortly, the distinction between the two former becomes manifest, while, between the cartilaginous layer and the fibrous sheath of the chorda, no line of demarcation can ever be perceived even with the aid of the microscope. Indeed these two latter tissues merge insensibly one into the other, so that in fragments of the sheath examined beneath the microscope, cartilage-cells may be observed scattered throughout its fibrous structure. Eventually this fibrous structure entirely disappears, and the whole sheath becomes cartilaginous; being thus converted, by change of tissue, into the bodies of the vertebræ. This account is in accordance with the observation made by Professor Müller,† that in some of the frog-like Amphibia and the Salamandrinæ, the ossification of the vertebræ takes place in the sheath of the cord. Coincident with the conversion of the sheath into cartilage, and the encroachment of this on the substance of the chorda, the cells of this substance gradually disappear and eventually are found only in the spaces between the bodies of the vertebræ. They are never directly converted into cartilage-cells.

Towards the end of the embryonic period of life cartilaginous rings begin to be developed also around the central parts of the nervous system lying in the axis of the embryo. These rings, which become the vertebral arches, result from the transformation of the internal portions of the two oval masses situated one on each side of the groove or canal containing the nervous centres. The remaining portions of the masses are converted into muscular tissue and integuments. The spinal chord also, as well as the chorda dorsalis, is provided with a kind of sheath, but not a fibrous one, such as is possessed by the latter structure.

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* Histoire Naturelle des Poissons d'eau douce, par M. Agassiz, t. i. p. 98; and Entwickelungs-geschichte der Geburtshelferkröte, p. 47.

† Physiology, p. 1613.

Development of the Vascular System.[*]

Formation of the Heart.—The account given by Reichert[†] of the mode of development of the heart in frogs, has been, for the most part, confirmed by the investigations of Vogt[‡] on the development of the toad, and those of Kölliker[§] on the development of the Batrachians generally. An almost similar mode of development is observed also in fishes, as shewn by the researches of Vogt on the development of the young salmon.[||] According to each of these observers, the heart, in its earliest formation, is composed of a solid compact mass of embryonic cells, similar to those of which the other organs of the body are constituted. It is at first unprovided with a cavity: but this shortly makes its appearance, resulting apparently from the separation from each other of the cells of the central portion. A liquid is now formed in the still closed cavity, and the central cells may be seen floating within it. These contents of the cavity are soon observed to be propelled to and fro with a tolerable degree of regularity, owing to the commencing pulsations of the heart.

These pulsations, according to Vogt, take place even before the appearance of a cavity, and immediately after the first "laying down" of the cells from which the heart is formed. Vogt has observed this especially in the embryonic salmon.[¶] At first the contractions seldom exceed from fifteen to eighteen in the minute. In the production of them, the whole mass of cells appears to be concerned, for in none of the individual cells is there ever observed either contraction or enlargement during the pulsations: although M. Dumesny[**] states, as the result of observations on the embryos of Pæcilia Surinami, that such contractions and dilatations of the several cells may be distinctly observed. The occurrence of contractions of the walls of the heart previous to the formation of any muscular or other contractile tissue has been observed also in the chick by MM. Prevost and Lebert.[††]

Probably by the metamorphosis of the contained cells, the fluid within the cavity of the heart shortly assumes the characters of blood. At the same time the cavity itself forms a communication with the great vessels in contact with it, and the cells of which its walls are composed are transformed into fibrous and muscular tissues, and into epithelium.

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[*] Müller's Physiology, p. 1620.

[†] Müller's Physiology, p. 1526.

[‡] Entwickelungs-geschichte der Geburtshelferkröte, p. 69.

[§] An. des Sc. Nat. 1846, Zoologie, p. 96.

[||] Hist. Nat. des Poiss. d'eau douce, par M. Agassiz, tome i. 1842, p. 181.

[¶] Op. cit. p. 182.

[**] An. des Sc. Nat. 1844, p. 344.

[††] Ibid. 1844, p. 302. A long account of the mode of development of the heart, and of the subsequent changes in its form, and in the relations of its several parts is contained in this memoir.

The development of the heart out of a solid mass of embryonic cells, and the early appearance of pulsations, has been described as occurring in Mammalia also, by Bischoff.[*]

The transformation subsequently undergone by the heart of the Mammalian embryo, and the mode in which its cavity is divided into its four compartments are described by Bischoff much in the same manner as they were by Rathke, Wagner, Meckel,[†] and others. (See fig. 19.) In his description also of the formation of the branchial arches and the arrangement of the first divisions of the aorta in the mammalian embryo, Bischoff agrees in all essential points with the accounts furnished by Von Baer,[‡] and other observers (see fig. 20), and with the more recent extended observations of H. Rathke.[§]

Fig. 19.[||]

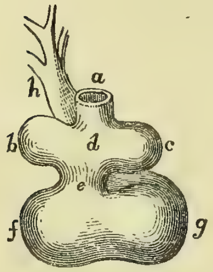
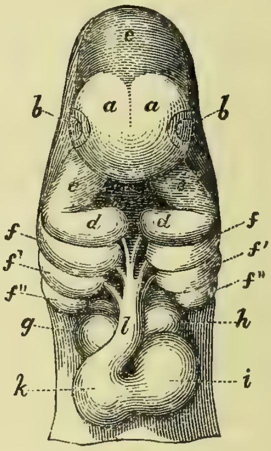


Fig. 20.[¶]



Development of Veins.—According to some recent researches by Professor Müller,[**] the posterior subvertebral veins, generally known as the vena azygos, and vena hemiazygos,[††] are the true analogues of the cardinal veins of Rathke, which are persistent in fishes. The union of these two conjugate subvertebral veins in the human subject, and the subsequent termination of the true vena azygos, thus formed, in the vena cava superior, is little more than a repetition of what occurs in the Myxionoid fishes, where the symmetry of the venous system observed in fishes generally is destroyed; the union of the anterior and posterior subvertebral trunks (the jugular and cardinal veins of Rathke) taking place on one side only, and the two posterior veins uniting before joining the single anterior trunks.

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[*] Entwickelungs-gesch. der Säugeth. und des Menschen, p. 236.

[†] Müller's Physiology, p. 1621. [‡] Ibid. p. 1624. [§] Müller's Archiv. 1843.

[||] Fig. 19. A posterior view of the heart of an embryo dog, representing the early division of this organ into its several cavities. *a*, the common venous trunk cut across; *b*, the left, *c*, the right auricular appendage; *d*, middle space between the two future auricles; *e*, canalis auricularis; *f*, the left, *g*, the right ventricle; *h*, trunk of the aorta with its first branches. After Bischoff. (Entwickelungs-geschichte des Hunde-Eies.)

[¶] Fig. 20. Embryo dog representing the visceral or branchial arches. *a* and *c*, the brain; *b*, rudimentary eyes; *d*, first visceral arch; *e*, continuation of the same: *f*, *f'*, *f''*, second, third, and fourth visceral arches; *g*, the right, *h*, the left auricular appendage of the heart; *i*, the left, *k*, the right ventricle; *l*, trunk of the aorta with its first branches forming the aortic arches. After Bischoff. Ibid.

[**] Vergleichende Anatomie der Myxinoiden, dritte Fortsetzung. Berlin, 1840.

[††] Physiology, p. 1625.

Development of Blood-vessels generally.—From his researches on the mode of development of the tissues in young Batrachians, Kölliker * has obtained some important results in relation to the formation of blood-vessels, which are especially valuable since they tend, in great measure, to reconcile the opposite opinions of those physiologists who adopt Schwann's view † in its fullest extent, by attributing the formation of blood-vessels exclusively to the direct transformation of nucleated cells, and of those who, with Plattner and others, consider that new blood-vessels are never formed except as off-shoots from previously existing vessels. Kölliker finds, that in the tail of tadpoles it is by the combined metamorphosis of cells and the production of off-shoots from tubes already in connexion with the general circulation, that new vessels are developed. In the tails of these larvæ all the vessels have originally the microscopic characters of the finest capillaries, being composed of a delicate, perfectly homogeneous membrane, with nuclei scattered along its internal surface. The mode of formation of the main arterial trunk and its corresponding vein, which run along the axis of the tail, cannot be observed, owing to the opacity of the surrounding tissues at the period of their development; but these two trunks, which at their distal extremity communicate with each other by a simple arch, elongate, as the tail increases in length, by pushing forth off-shoots which join and coalesce with embryonic cells situated around the posterior extremity of the chorda dorsalis. The first lateral vessels of the tail have the form of simple arches, passing from the artery to the vein, and are produced by the junction of prolongations sent from both the artery and vein, with certain elongated or star-shaped cells, in the substance of the tail. When these arches are formed, and are permeable to blood, new prolongations pass from them, join other radiated cells, and thus form secondary arches. In this manner the capillary net-work extends in proportion as the tail increases in length and breadth, and it, at the same time, becomes more dense by the formation, according to the same plan, of fresh vessels within its meshes. The prolongations by which the vessels communicate with the star-shaped cells, consist at first of narrow pointed projections from the side of a vessel, which gradually elongate until they come in contact with the radiated processes of the cells. The thickness of such a prolongation often does not exceed that of a fibril of fibrous tissue, and at first it is perfectly solid; but by degrees, especially after its junction with a cell, or with another prolongation, or with a vessel already permeable to blood, it enlarges, and a cavity then forms in its interior. Both the enlargement and hollowing out of the branch commence at the point of its departure from the vessel on the one hand, and at its point of junction with the cell on the other hand: the consequence of which is the appearance of great irregularity in the form and size of these various capillaries at their first formation. (See fig. 21.)* Of the star-shaped cells described by Schwann as being so numerous in the substance of the tail of young Batrachians, only a few are developed into blood-vessels, others are converted into lymphatic vessels, others into nerves, while many do not appear to undergo any metamorphosis.

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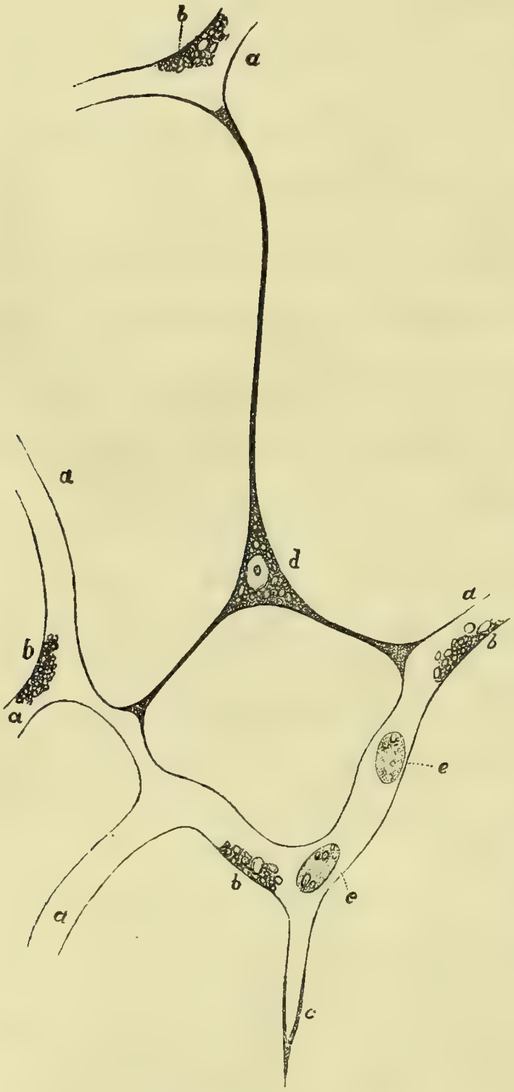
* An. des Sc. Nat. Août, 1846.

† See Müller's Physiology, pp. 404, and 1537.

Fig. 21.†



Plattner,‡ whose observations were made also on the tail of the tadpole, appears to have seen the formation of new vessels only as effected by the junction and coalescence of off-shoots from previously existing vessels. He observes that in this growing structure there may frequently be seen abrupt closed extremities of capillaries, and that sometimes long narrow processes may be noticed issuing from these extremities, and either gradually disappearing or seen uniting with other similar processes from neighbouring vessels, so that two such form by their union one arch which gradually enlarging and becoming permeable to blood corpuscles, constitutes a new capillary loop. A very similar account of the mode of production of new vessels in the tail of tritons and tadpoles is given also by MM. Prevost and Lebert,[*] who, with Plattner, are of opinion that such vessels are always formed centrifugally, and under the influence of the circulation, by arches passing from a minute artery to a corresponding vein. These arches, they state, are formed in spaces left by the separation of the cells of the part in which the development of vessels takes place, and do not result as Schwann and Kölliker describe, from the coalescence of the branches proceeding from cells. The circumstance which, in their opinion, has led to the supposition of this latter being the true mode of formation, is the resemblance to cells presented by the interspaces themselves. From their observations on the development of the chick also,[†] Prevost and Lebert arrived at similar conclusions concerning the formation of blood-vessels.

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* A very similar process to that above described is found by Kölliker to take place also in the development of the blood-vessels of the Sepia. Entwickelungs-geschichte der Cephalopoden, pp. 82-3.

† Fig. 21. Capillary blood-vessels of the tail of a young larval frog. Magnified 350 diams. After Kölliker. *a*, capillaries permeable to blood; *b*, fat granules attached to the wall of the vessels, and concealing the nuclei; *c*, hollow prolongation of a capillary, ending in a point; *d*, a branching cell with nucleus and fat-granules; it communicates by three branches with prolongations of capillaries already formed; *e*, blood-corpuscles still containing granules of fat.

‡ Müller's Archiv, 1844.

In the opinion of Vogt also, from observations made on the embryonal salmon,[‡] blood-vessels invariably originate, not from the branching and coalescence of cells, but as spaces or channels hollowed out in the midst of the cell-substance of the part in which the development takes place. The formation of these channels appears, however, in his opinion, to result from a simple separation of the cells from each other, and, contrary to the view of Plattner, Prevost, and Lebert, to be quite independent of the heart or the rest of the circulation, with neither of which, indeed, have the channels at their first formation, any communication. At first these channels are unprovided with distinct bounding walls, but shortly there is observed a delicate membranous lining to the canal, formed apparently by a layer of the cells in the midst of which the new vessels are developed. This mode of development, according to Vogt, is observed in the formation both of the first embryonic trunks in connection with the heart, and of the finer vessels or capillaries in other parts. That it prevails in the first case, is admitted also by Kölliker,[§] but that it does not, in his opinion, in the case of the finer vessels, has been already shewn.

The description which Kölliker has given of the process as it occurs in the tail of young Batrachians, is doubtless the most correct one, and it may, with every probability of truth, be assumed to represent the mode in which blood-vessels are developed in all other tissues, and in all other classes of animals. With Kölliker's account it is possible to reconcile the descriptions furnished by Plattner and others, even though contrary to the designs of the authors; for with the exception of admitting the influence of cells, their account of the gradual formation of arches by the junction and coalescence of fine processes, and the gradual conversion of these into permeable tubes, closely accords with that given by Kölliker. The description furnished by Vogt is, however, so much opposed to that of Kölliker, that the difference must either be attributed to some misconception of appearances by this usually most accurate observer, or, what is less probable, to the existence of another process less simple than the former, by which also the development of blood-vessels may be effected. Of the correctness of Kölliker's account, the writer can speak with complete certainty, from having, in some investigations with Mr. Paget, observed an almost exactly similar series of changes in the fine gelatinous tissue conveying the umbilical vessels of a sheep's embryo seven lines in length to the uterine cotyledons. Perhaps no better tissue than this could be selected for witnessing the mode of development of blood-vessels, for it is exceedingly fine, transparent, and composed almost entirely of a homogeneous substance, in which numerous scattered cytoblasts and cells, with developing blood-vessels, are almost the only objects seen. In some portions the development of vessels is complete, networks of various sized tubes filled with blood-corpuscles alone appearing. But in most other portions, together with completely formed and permeable vessels, the various steps in the development of these from elongating and branching cells, are distinctly seen. In such places are observed chains and networks of cell-like bodies, mostly filled with granular matter, and occasionally presenting a clear oval nucleus, and connected to each other by exceedingly slender filaments, some of which appear tubular, and in many instances are connected with blood-vessels of considerable size (see fig. 22). The cell-like bodies thus connected are of various shapes, most of them round or oval, many very narrow and spindle-shaped, some angular and elongated from their angles. The threads of connection are attached to the angles and points of the elongated bodies, and in the case of the round and oval ones, are so attached that these bodies appear like varicose or aneurismal enlargements. The various transitional states, from the fine solid threads of connection, to permeable tubules containing one or more rows of blood-corpuscles, are very manifest. As observed by Kölliker, the formation of a tubular cavity in the filaments appears, though not invariably, to commence at the points of their attachment to permeable blood-vessels and to the cell-like bodies. Occasionally blood-corpuscles may be traced

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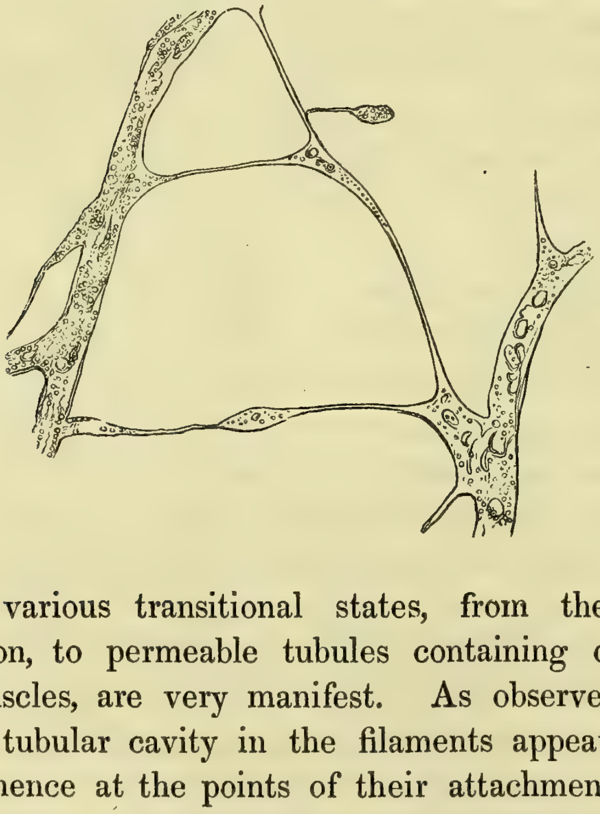
[*] Ann. des Scien. Nat. 1844, p. 222.

[†] Ann. des Scien. Nat. 1844, p. 265.

[‡] Hist. Nat. des Poissons, t. i. p. 206 ; and Entwickel. der Geburtshelferkröte, p. 71.

[§] Henle and Pfeufers Zeitschrift für rationelle Medizin, 1845-6.

Fig. 22.*



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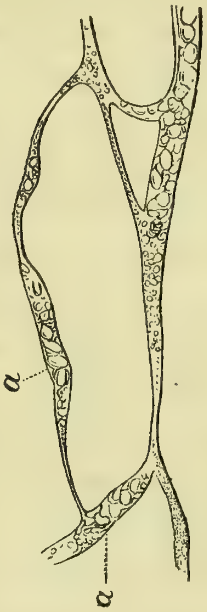
* This and the following figure, for the use of which the writer is indebted to the kindness of Mr. Paget, represent several of the appearances described in the text.

for a short distance down one such filament in connection with a vessel, and then observed to cease abruptly at a part where the filament becomes impermeable, and this apparently not from collapse of its walls, but either from no tubular cavity at all, or only an exceedingly narrow one, having yet been developed in its fine thread-like structure. In other instances isolated parts along the course of the fine filaments appear first to have become hollow, for here and there are observed isolated groups of coloured nucleated blood-corpuscles in distended parts of the narrowest tubes (*a a*, fig. 23). This circumstance would seem to prove that just as the heart and first blood-vessels are developed independently of each other, so may perfect blood-corpuscles be developed in parts not in immediate connection with the already formed vascular system, and from other materials than those derived directly from the contents of the blood-vessels; for in several of the instances in which the above peculiarity was observed, the part containing corpuscles was connected at either extremity with a blood-vessel or an elongated cell only by an exceedingly fine filament, which appeared quite incapable of transmitting a particle of even much less size than a blood-corpuscle. The walls of the fine tubes, as was observed by Kölliker, appear to be formed of the membrane of the cell which is drawn out into the elongating filaments proceeding from these bodies: in structure it appears quite homogeneous. The large vessels possess delicate membranous walls with a fine, longitudinally fibrous structure, and, as noticed by Kölliker, with scattered nuclei imbedded in their substance.*

Fig. 23.



Development of Lymphatics.—The mode of development of lymphatic vessels, which has hitherto been involved in complete obscurity, appears to be now fully elucidated by the researches of Kölliker on the formation of the tissues in young Batrachians.† This laborious investigator has found that these vessels are developed in a manner almost precisely similar to that pursued in the development of blood-vessels, namely, by the junction and fusion of processes from star-shaped cells with each other, or with off-shoots proceeding from already formed vessels. The chief point in which the development of lymphatics differs from that of blood-vessels, is in the processes from the cells, and from already formed vessels, uniting directly with each other, and thus producing a tube which does not give off lateral communications so as to form a network; for the lymphatics, at their first formation, as in their perfect state, are distinguished from blood-vessels by the rarity of their anastomoses.

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* The chief interest of the above observations is in their proving that the blood-vessels in Mammalia are developed after a plan exactly similar to that observed by Kölliker in Reptiles.

† An. des Sc. Nat. 1846, p. 99.

Development of the Nervous System.[*]

First Traces of the Nervous System.—As was before observed (page 84) the account given by Reichert of the original formation of the central parts of the nervous system has been considerably modified by the investigations of Bischoff on the development of Mammalia.[†] The two oval masses or laminæ, between which the primitive groove is situated, are not, as was shewn also by Von Baer, the parts out of which the nervous system alone is formed, but are for the most part merely the foundations for the formation of the dorsal part of the trunk of the body, the central nervous system being developed only from that portion which immediately borders upon the primitive groove. Concerning the time at which this development first presents itself, Bischoff offers a somewhat different account to that given by Von Baer, who was of opinion that it did not commence until after the conversion of the groove into a canal by the junction of the lateral masses on each side of it. But Bischoff states that previous to the formation of a canal, nervous substance is developed along the whole inner surface of the groove, and apparently by a metamorphosis of the portions of the lateral masses immediately contiguous to the groove. The substance composing these portions gradually assumes a pellucid aspect like nervous substance, and increases in quantity : the inner border of each mass thus altered, then approximates and gradually unites with its fellow of the opposite side, so as to convert the previous groove into a tube, the walls of which thus consist of nerve-substance, while the hollow axis constitutes the central canal of the spinal cord. The approximation and union of the margins of the groove takes place first about the middle of the groove, and then proceeds upwards and downwards from this point. At the commencement of this union at the middle part of the groove, the upper or cephalic is formed (as was shewn also by Reichert in the chick)[‡] into three successive dilatations which are the vesicles from which the brain is formed. At the opposite or caudal extremity the groove presents a lancet-shaped dilatation : this corresponds to the future Cauda equina (or Sinus rhomboidalis, as it is named in birds, *vide* fig. 11, p. 84). That the two oval masses bounding the primitive groove do not constitute the rudiments of the central parts of the nervous system, is shewn to be the case in Amphibia also, from the result of Vogt's investigations on the development of the toad.[||] In this amphibious animal, he finds, as Bischoff has found in Mammalia, that the central nerve-substance is developed as a very thin layer which separates from the sides and bottom of the primitive groove; but contrary to Bischoff's observations, he states that the formation of nerve-substance does not take place until the primitive groove is converted into a canal by the junction of the margins of the lateral masses of cell-substance by which it is bounded.

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[*] Müller's Physiology, p. 1627.

[†] Entwickelungs-gesch. der Säugeth. und des Menschen, p. 165, *et seq.*

[‡] Müller's Physiology, p. 1547.

[||] Entwickelungs-gesch. der Geburtshelferkröte, p. 66.

Development of cerebral hemispheres.—It is stated by Professor Retzius* that the three portions of the cerebral hemispheres in the human embryo are developed, not at once, but at three separate periods. In the first of these periods, which extends from the second to the third month, the anterior lobes are formed; during the second period, which is comprised between the end of the third and the beginning of the fifth month, the middle lobes are formed; after this, therefore last of all, the posterior lobes are developed,

The inferior horns of the lateral ventricles and the hippocampi do not appear until the second period; at this period also the optic thalami make their appearance, and after these the tubercula quadrigemina.

Development of the Alimentary Canal.†

A somewhat different account of the mode of development of the Alimentary system of the toad to that given by Reichert‡ of the same process in the frog, has been furnished by Vogt.§ In the opinion of the former observer, the Alimentary canal is formed from the central cells of the yolk, but according to Vogt, it is formed from the internal or so called mucous layer of cells of which the germinal membrane or cortical part of the yolk is composed. On making a longitudinal section of the embryo and yolk through the chorda dorsalis, at the time of the formation of the branchial arches, the central part of the yolk (dotter-kern) is observed as a loose globule surrounded by a tolerably thick layer of cortical cell-substance. In the midst of this cortical layer the chorda is imbedded, being separated from the nucleus (or central part) of the yolk by a considerable quantity of the cells. In front, immediately beneath the elongated cephalic portion of the axis, there is observed a slight depression, which is the rudiment of the cavity of the mouth. At this time no separation of the cortical layer of cells into serous and mucous laminæ has taken place. As the growth of the branchial arches developed from the undivided cortical layer proceeds, the portion of the yolk-nucleus corresponding to the rudimentary mouth becomes depressed. The division of the germinal membrane into its serous and mucous layers now gradually commences. The latter separates itself from the former over its whole extent, except at the part corresponding to the rudimentary mouth, that corresponding to the anus, and along the entire vertebral line. While this separation is taking place, masses of cells from the mucous layer are left between the two laminæ; from these the liver and the Wolffian bodies are formed. When thus separated from the serous layer, the mucous layer forms a completely closed sac containing the yolk-nucleus. Shortly, over its whole external surface, there is developed a fine layer of cells, which at the above-mentioned points of attachment, becomes continuous with a similar layer of cells simultaneously developed along the inner surface of the serous lamina; and from these united layers of cells are subsequently formed the peritoneal sac and the mesentery. By the absorption of the membranes at the points corresponding to the cavity of the mouth and the anus, the sac formed by the mucous layer is opened, and the character of the Alimentary canal is thus assumed by it. During the subsequent growth of the intestine the

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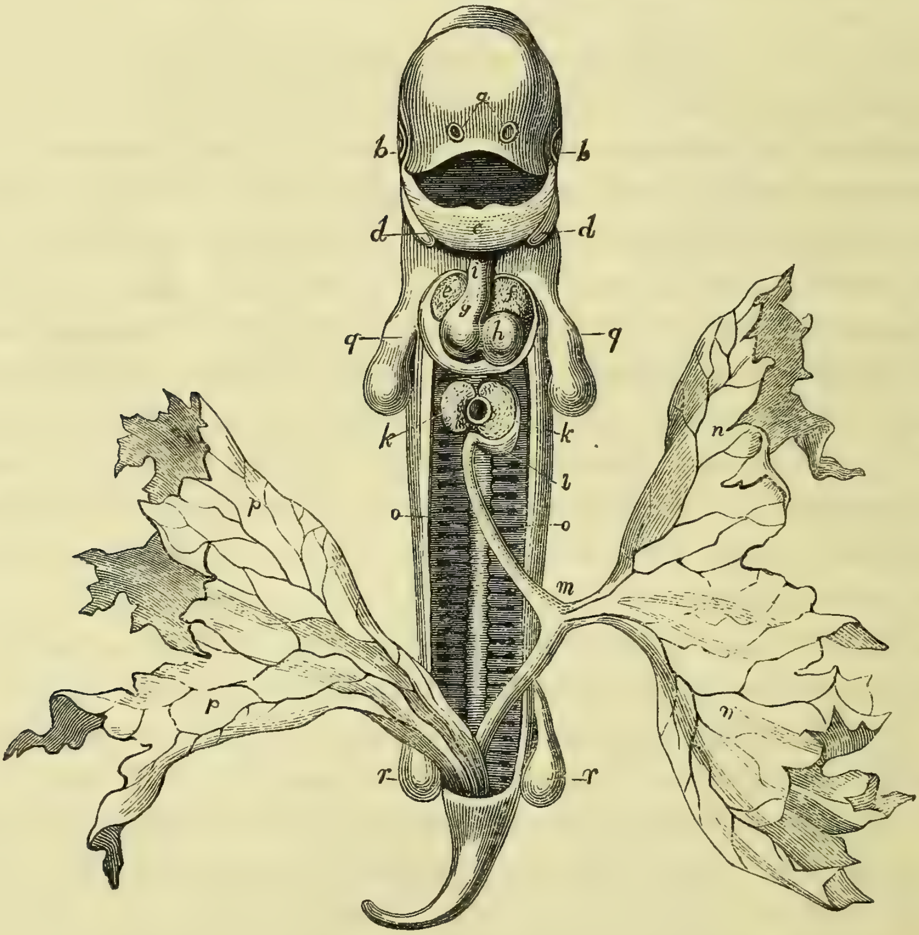
* Arch. d'Anat. Gen. et de Phys. Janvier, 1846, p. 24.

† Müller's Physiology, page 1633.

‡ Ibid. p. 1527.

§ Entwickelungs-ges. der Geburtshelferkröte, p. 67.

Fig. 24.*



* Fig. 24. An embryo dog representing the junction of the umbilical vesicle with the intestinal canal. *a*, rudimentary nostrils; *b*, rudimentary eyes; *c*, the first visceral arch; *d*, the second visceral arch; *e*, the right, *f*, the left auricular appendage; *g*, the right, *h*, the left ventricle of the heart; *i*, the aorta; *k*, the liver, between the two lobes of which is perceived the divided orifice of the omphalo-mesenteric vein; *l*, the stomach; *m*, the intestine, communicating with the umbilical vesicle *n*; *o*, the Wolffian bodies; *p*, the allantois; *q*, the upper extremities; *r*, the lower extremities. After Bischoff. (Entwick. des Hunde-eies.)

central yolk-cells, which lie free in the cavity, and are not attached to its internal surface, gradually, and at length completely, disappear. They are not directly converted into the cells of the mucous membrane of the intestine.

With regard to the first formation, and subsequent development of the intestinal system in Mammalia, the account given by Bischoff is in close accordance with that furnished by Von Baer.* (See fig. 24.) The process pursued is very similar to that which takes place in the development of the intestine in the chick.†

Digestive Glands.—The account given by Professor Müller‡ of the mode of development of the large glands opening into the intestinal canal, as the liver and pancreas in birds, has been for the most part confirmed by Bischoff, in the case of Mammalia.§ The salivary glands also pursue a similar mode of development.‖

Development of the Respiratory Apparatus.¶

Thymus Gland.—The development of the thymus gland has been investigated by Mr. Simon.** The earliest form in which he has discovered it, in the embryos of swine and oxen (on which animals his researches were, for the most part, made), is that of a simple tube, lying along the carotid vessels, and surrounded by faint indications of nascent areolar tissue. The contents of the tube are granular and dotted; its membrane is constituted of a fine, transparent, homogeneous tunic, presenting, at regular intervals, slight elongated thickenings of its substance, which are probably the remains of nuclei of primordial cells from the coalescence of a linear series of which it is most likely the tubule is originally formed. The second stage in the process of development is very analogous to the mode of growth attributed to true glands: the tube bulges at certain points of its length on one side or the other, and gives origin to diverticula or follicles, which maintain their connection with its cavity; and are filled with the same contents and bounded by the same transparent membrane as the tubule itself. Slight differences are observed in the mode in which these diverticula are formed, and in the rapidity with which the process takes place at different parts of the gland, but they always tend to assume a more or less spherical form, and to retain their connexion with the main canal by means of a narrow isthmus of communication. In the further growth of the gland secondary and tertiary hollow projections extend from each of the primary follicles, and by a continuation of the process, new groups of follicles are successively formed, and, thus the gland attains the size and apparently complex structure which distinguish it in the mature fœtus. Each of the new follicular or vesicular off-shoots, maintain, like the first, a free communication with the primary tube, although in the fully-developed glands this is difficult to be shewn.

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* Müller's Physiology, p. 1568, and fig. 208.

† Ibid. p. 1540.

‡ Physiology, vol. i. p. 489.

§ Op. cit. p. 322.

‖ Page 323.

¶ Müller's Physiology, p. 1634.

** A Physiological Essay on the Thymus Gland. London, 1845, 4to.

Development of the Wolffian Bodies, Urinary Apparatus, and Sexual Organs.[*]

Wolffian Bodies.—In his account of the development and relations of the Wolffian bodies in Mammalia, Bischoff,[†] for the most part, agrees with Professor Müller[‡] in his description of these bodies, though in some particulars he differs from him. Like Müller and Von Baer, he describes the corpora Wolffiana as double organs from their first formation, and states that he has examined them in several Mammalian embryos, at an age at which they could be perceived only with the microscope, but that they never appeared to proceed from an originally single organ, as is said by Rathke to be the case in birds.[§]

Although Bischoff is opposed to Reichert's view,[||] that the allantois is developed from the corpora Wolffiana,—having shewn, as already observed (page 86), that, in all the Mammalian embryoes which he had examined for the purpose, the development of the allantois takes place before any trace of the Wolffian bodies can be perceived—yet he maintains, as has been since done by Langenbeck (page 88), that when these bodies are formed, their excretory ducts communicate directly with the allantois. Indeed, this view is now admitted by most physiologists.

According to Professor Müller,[¶] the excretory duct of each Wolffian body in Mammalia proceeds from the lower extremity of the organ instead of running along its outer side as is the case in birds: the filament along the outer side of the Mammalian Wolffian body which appears to correspond to this excretory duct in birds, being, in Professor Müller's opinion, the Fallopian tube in the female, the vas deferens in the male. Bischoff, however, agrees with Oken and Himly that this latter filament contains in Mammalia as well as in birds, the true excretory duct of the Wolffian body; having injected the organ through the duct in this filament, and having also succeeded in forcing by compression the contents of the organ into it. As well as containing the excretory duct of the Wolffian body, however, this filament also contains (as Müller said) the tube which passes to the rudimentary testis or ovary, and which in the male becomes the Vas deferens, in the female the Fallopian tube.[**]

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[*] Müller's Physiology, p. 1635.

[†] Entwickelungs-gesch. der Säugeth. und des Menschen, p. 340–9.

[‡] Physiology, pp. 1635-40.

[§] Beiträge zur Geschichte des Thierwelt. t. iii. p. 50.

[||] Müller's Physiology, p. 1554.

[¶] Physiology, p. 1637.

[**] Bischoff, op. cit. p. 371.

Concerning the use of the corpora Wolffiana no doubt now exists of their being organs for the elimination of the urinary secretion during the early periods of embryonic life, and thus temporarily discharging the functions of the kidneys, which are not developed until a later period. Bischoff has detailed all the conclusive evidence in favour of this view.

Dr. G. L. Kobelt has recently published an essay,* the chief object of which is to shew, that, contrary to the opinion of Professor Müller,† and most other physiologists, the Wolffian bodies do not in either sex disappear during, or after, intra-uterine life, but that in the male sex most of the middle tubes of each Wolffian body become joined to the coni vasculosi of the testicle and so constitute the epididymis, while in the female sex also these bodies persist during life in the form of a structure closely analogous to the epididymis, and attached to the ovary.

Ovaries and Testes.—Bischoff‡ observes, that in Mammalian embryoes the ovaries and testes do not appear until some time after the formation of the other chief organs, and after the Wolffian bodies have made considerable progress in their development. They make their appearance, however, before the kidneys. As remarked, also, by Valentin, no difference in structure can be discerned between the testes and ovaries at their first formation. According to Valentin's account of the formation of the tissue of the testis,§ the first traces of the tubuli seminiferi appear in the form of transverse lines or streaks on the surface of the organ. These divide into narrower striæ which are subsequently converted into the seminiferous tubules. Bischoff,|| however, is opposed to this view of the development of the seminiferous tubules, and is of opinion that they are formed from nucleated cells which arrange themselves in linear series, and become fused at their opposed surfaces, in a manner similar to that which he considers to be pursued in the formation of the uriniferous tubules of the kidney.¶ For Valentin's account of the formation of the tissue of the ovary, and for Bischoff's opinion of this account, see page 36.

Rudimentary Uterus in the Male.—In the account given by Professor Müller ** of the mode in which the sinus urogenitalis of the early embryo is subsequently divided into two portions, pars urinaria, and pars genitalis, it is stated that while the former is converted into the urinary bladder the latter is transformed into the vesiculæ seminales in the male, and into the uterus in the female. In relation to this subject an interesting fact has been discovered by Professor E. H. Weber,†† namely, that in the males of several mammiferous animals which he examined, and in man, the organ analogous to the female uterus which is formed in

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* Der Neben-Eierstock des Weibes, &c. Heidelberg, 1847.

† Physiology, p. 1637.

‡ Entwickelungs-gesch. des Säugeth. und des Menschen, p. 355.

§ Entwickelungs-geschichte, p. 391.

|| Op. cit. p. 357.

¶ Page 354.

** Physiology, p. 1639.

†† Zusätze zur Lehre Vom Baue und Verricht. der Geschlechts-organe, p. 11.

the embryo, persists in a more or less developed state, throughout the whole of adult life. In man this rudimentary uterus exists in the form of a somewhat oval vesicular body imbedded in the substance of the prostate gland: a portion of it projects as a narrow ridge along the middle of the lower surface of the prostatic portion of the urethra, and is commonly known as the *caput gallinaginis* or *verumontanum*. That it is a hollow body, and has no communication with the prostate, may be shewn by inflating it with air. Very commonly the orifice of this, which Weber calls the male uterus, remains patent and may be discerned on the middle line of the urethra between the openings of the two ejaculatory ducts; sometimes it is very narrow, and in a few cases is even entirely closed. The male uterus is still more manifest in the beaver, where it is found enclosed within a fold of the peritoneum, and situated between the urinary bladder and the rectum, exactly in the position occupied by the uterus in the female beaver: in the male, also, as in the female, this organ is two-horned. Likewise in the male rabbit a rudimentary uterus exists and occupies the same situation as the fully developed organ of the female.* The Vasa deferentia open into the lower part of this male organ just as their analogues the Fallopian tubes open into the upper part of the female uterus. It has also been found by Weber that the walls of this rudimentary uterus possess distinct muscular fibres, and moreover that when mechanically or electrically irritated they contract and manifest distinct peristaltic movements.

In the newly-born rabbit, the organs of generation, both external and internal, so closely resemble each other in the two sexes, that it is only possible to distinguish the male from the female by the manner in which the Vasa deferentia differ from the Fallopian tubes. A male rudimentary uterus has also been found by Weber, in the dog, cat, sow, and horse. In the three former animals the orifice of the uterus usually appears closed: but in the horse, as in man, it is frequently found open.

The permanent existence of a rudimentary uterus in the male, accounts satisfactorily, in Weber's opinion, for the presence of a large uterus in the so-called male hermaphrodites of the human subject; such a uterus is of course only the vesicula prostatica, or rudimentary uterus, in a more fully developed state.

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* Weber's observations have been confirmed by Huschke. Lehre von Eingeweid. des Menschl. p. 410.

DEVELOPMENT OF THE ANIMAL TISSUES.*

It is proposed in the following pages to offer some account of the present condition of the theory of cell-development, especially in relation to the following points :—

1. The nature and composition of the several parts of which a cell is constructed.

2. The order in which these several parts are developed in the formation of cells.

3. The manner in which the multiplication of cells is effected.

4. The transformations undergone by cells in the development of tissues.

1. Very little requires to be said concerning the *composition of the cell* itself. Its membrane or wall appears, by almost universal assent, to be formed of a protein-compound, most probably of albumen, except in a few cases in which it seems to be composed of a substance more allied to fibrine.† Although the cell-wall is rendered transparent and indistinct by acetic acid, yet it is not dissolved by this reagent, as is usually supposed to be the case, for on the addition of an alkali, such as a solution of potash or ammonia, its form and other external characters are in many cases restored.‡ With respect to the *contents* of cells, it is perhaps sufficient to state that further investigations continue to shew how various these may be, the varieties being as numerous as the functions which the cells discharge, and often differing in the same cell at different periods of its life. These contents, although occasionally composed of a clear fluid of various consistency and colour, are usually more or less granular, the granules consisting of different colouring matters, of fat particles, and of a fine molecular substance, whose nature is still obscure.

There is much discrepancy in the accounts given by different writers concerning the composition and general characters of the *nucleus.* This discrepancy is probably in great measure due to the fact, that after their formation the nuclei undergo various alterations in aspect if not in composition, and in some measure also to the fact of there probably being some original differences in the nuclei of different cells. Sometimes the nucleus occurs as a more or less solid body of a granular aspect, while at other times it appears as a pale vesicle with a distinct cell-wall and fluid contents. And between these two conditions varieties are occasionally found which would seem to prove that the one is only a modification of the other, and that these several varieties represent so many transitional stages between the two. The pale vesicular form is by far the most general one, and in Kölliker's opinion,* is the constant form of the nucleus in the early stages of the cell's life. It has been long known that the nucleus has a different composition to that of the cell, many agents which act upon the one having no effect upon the other. Kölliker† is of opinion that the membrane of the vesicular nucleus is composed of pyin, the clear contents of albumen, and the nucleolus of fat. His opinion that the membrane is composed of pyin, is derived chiefly from the fact of the nucleus being insoluble in acetic acid, a property which is possessed by no other nitrogenous compound except chondrine;‡ and this substance is soluble in the gastric fluid, while the nuclei are not, neither is pyin. The presence of albumen in the contents of the vesicular nuclei he thinks is proved by the contents of the germinal vesicle (which he considers to correspond to the so-called nucleus of other cells) being rendered granular by ether. The fatty nature of the nucleolus is indicated by its aspect, and by the presence of fat in parts composed chiefly of cells.

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* Müller's Physiology, p. 1641.

† Kölliker, Entwickelungs-geschichte der Cephalopoden, p. 154.

‡ Donders, Holländische Beiträge zu den anat. und physiol. Wissenschaften, 1846.

Schleiden§ described the nucleus in the cells of plants as being invariably situated within the substance of the cell-wall, which at that point divides into two laminæ, between which the nucleus is placed. In animals also the nucleus is commonly situated at the wall of the cell, sometimes apparently imbedded in its substance, but according to Schwann,‖ most frequently attached to its inner surface, and never invested internally by a layer of the cell-wall as it is in plants, according to Schleiden. Henle¶ states that sometimes, as in pigment-cells and the cells of the crystalline lens, the nucleus is situated outside the cell-wall, which at that part presents a shallow depression to receive it; but Dr. Sharpey** is inclined to doubt the exterior position of the nucleus in these cases. Occasionally the nucleus is situated towards the centre of the cell,†† as is well shewn in the cells of cylinder-epithelium.‡‡ In such cases, however, the nucleus does not usually appear to lie free in the cavity of the cell, and to admit of being altered in position as the cell rolls over, but it seems to be quite fixed, and probably adheres to the internal surface of the cell-wall which, in cylindrical cells, closely surrounds it in one plane, and in flat cells is in contact with it at opposite sides. It was stated by Hewson,§§ however, that when the nucleated blood-corpuscles of fish or reptiles are swollen with water, and watched when rolling over, the nucleus may be distinctly seen to fall from side to side in each distended corpuscle; and Schultz [*] appears to have recently advanced a similar opinion. But Henle[†] remarks that he has never been able to witness this phenomenon, and he considers the nucleus of blood-corpuscles, as also those of mucus-corpuscles and epithelium-cells, to be attached to the inner surface of the cell-wall.

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* Entwickelungs-geschichte der Cephalopoden, p. 142.

† Op. cit. p. 144–5.

‡ And according to Kölliker, fibrine, but in this he is manifestly wrong.

§ Müller's Archiv. 1838, p. 148.

‖ Microscopische Untersuchungen, p. 210.

¶ Allg. Anat. p. 192.

** Quain's Anatomy, Fifth edition, p. xliii.

†† In the case of vegetable cells, M. Mohl believes that the nucleus is invariably central at the earlier periods of the cell's life, and that its parietal position, when it occurs, is only a secondary state. (Botanische Zeitung, 1846; and Taylor's Scientific Memoirs, vol. xviii. 1846.)

‡‡ See Müller's Physiology, Second edition, p. 418, Fig. 36, B and C.

§§ Works, edited for the Sydenham Society by Mr. Gulliver, p. 222.

The nature and composition of the *nucleoli*, or nucleus-corpuscles, still remain obscure. Henle [‡] is doubtful whether what have been described as nucleoli may not be merely spaces in the interior of the nucleus. He thinks that this view of their nature is supported by the circumstance of no apparent chemical difference being perceived between them and the nuclei; agents which destroy the one, invariably destroying the other also. Vogt,[§] although he admits the real existence of nucleoli, usually of a vesicular character, yet agrees with Henle in regarding them as unessential elements of a cell. He states that when they appear, it is only at a late period of the cell's life, and that shortly after their formation they usually assume a vesicular character, and as they enlarge are probably developed into cells at the expense of the nucleus which they gradually destroy. Kölliker,[||] however, entertains an entirely different view of the nature and importance of the nucleoli. In his opinion, the nucleus ought to be regarded as a primary nucleated cell, and the structure usually called a primary cell as a secondary cell. In the formation of such primary cell (the nucleus of other writers) he believes that a round, dark, apparently homogeneous substance is first developed in the formative fluid. Around this body, which by him is regarded as the nucleus, by others as the nucleolus, the wall of the primary cell is gradually developed. Occasionally two, more rarely three, and still more rarely four, dark particles are found in a single primary cell (nucleus). Whatever may be the number, one at least is invariably found in every such cell up to a certain period of its growth. When single, the particle is situated on the wall of the cell; when there are several particles, they may occupy a similar situation, or be free in the cavity of the cell. Occasionally one or two particles apparently identical with these are found also among the contents of the secondary cells (or primary cells of other writers). They have all the appearance of being composed of oil or fat. Indeed, they appear to be identical with the elementary granules commonly found in the cytoblastema, and which Henle (as well as others) describe as minute vesicular-looking particles of fat. And it is difficult to determine in what respect they differ, and why Henle should discard the use of the term nucleoli; for, as will be presently shewn, he admits the importance of the elementary granules in the first formation of cells. Kölliker confirms Vogt's statement that the nucleoli are sometimes developed into vesicles, which then enlarge, apparently at the expense of the nucleus which disappears when these vesicles have attained a certain size, the vesicles themselves likewise disappearing soon afterwards. But in other cases, as will be presently shewn, the nucleolus, instead of disappearing, becomes constricted in the middle, and subsequently divided into two equal portions, around each of which a new cellular body or nucleus is then developed.* In all those cases, however, in which the nucleus or cell undergoes transformation into a higher tissue, the nucleolus disappears.† But this is certainly not invariably the case, for in the persistent nuclei of capillary blood-vessels, of the sarcolemma, and of several other tissues, a small dark particle, apparently identical with the nucleolus, may usually be observed.

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[*] Henle's Allg. Anat. p. 192.
[†] L. c.
[‡] Op. cit. p. 151.
[§] Entwickelungs-geschichte der Geburtshelferkröte, p. 118.
[||] Entwickelungs-geschichte der Cephalopoden, p. 149.

2. In considering the various modes in which the *development of cells* in the formative fluid or cytoblastema is effected, it must be remarked, in the first place, that it appears immaterial to the process in what part the formative fluid is situated. The same succession of changes in the formation of cells seems to be pursued whether the process occurs in the cytoblastema of the early ovum, in the secondary cytoblastema from which the several embryonic tissues are produced, or in the organisable material effused from the blood-vessels into the interstices of the various parts of the growing or adult body. The fluid in each case appears to possess the same formative properties, and the chief or only difference observed in the process relates to the mode in which the cells are ultimately disposed of. In the increase, also, of cells, by endogenous multiplication, the formative fluid out of which the young cells grow, so far as concerns its power of producing new cells, appears to be essentially the same as the cytoblastema elsewhere: and the differences in the mode of growth are probably more apparent than real, the developing cells in the one case lying free in the interstices of parts, in the other case being enclosed within a membranous envelope or parent-cell.

In the opinion of Schwann the development of cells pursues an almost exactly similar course in every case; and he believes that the subsequent multiplication of animal cells, is usually effected by the same series of changes as are undergone in their original development, the endogenous mode of origin so common in vegetable structures being rarely pursued in animal tissues. But, as will be presently shewn, the result of more recent investigations have made it probable that this mode of origin, or rather of multiplication, is of more frequent occurrence than Schwann supposed. The plan of cell development recognised by Schwann, is detailed in Professor Müller's Elements of Physiology.‡ In addition to this, the ordinary mode of development, Schwann also suggested the probable occurrence of a variety, or modification of it in some cases. For having observed that occasionally the nucleus of a cell contained two nucleoli, he thought that the circumstance might be explained by conceiving that two (or more) contiguous nucleoli, with their layer of granular deposit, had fused together before either of them had attained such a stage of development as singly to constitute a nucleus. And in those cases in which the nucleus of a cell appears to consist of two or more portions, he inferred that the component parts were so many nuclei which had been contiguous to each other, and fused together before the growth of the cell-wall around each had made much progress.

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* Kölliker, op. cit. p. 150.

† Op. cit. p. 151.

‡ Pp. 398 and 1641.

According to Henle* the formation of cells takes place in three different ways; in two of these (which appear to be only modifications of each other) the nucleus is developed first, while in the third it is not formed until after the cell, or even does not appear at all. In whichever of these ways the cells are developed, numerous spherical or oval fat-like particles first make their appearance in the cytoblastema or formative fluid. In one of the three modes of development, a layer of the dimly-granular material of the cytoblastema appears to deposit itself upon one of these fat-like particles, and thus to form a nucleus, upon which a cell-wall then grows, though, as will be noticed again presently, in a manner somewhat different from that pointed out by Schleiden and Schwann. In another mode, the nucleus is formed by the grouping together and coalescence of two, three, or even four of the elementary particles; a cell-wall is developed around this compound nucleus in the same manner as around the simple one. As the growth of the cell proceeds, the component particles of the nucleus become completely fused together, and a single smooth body eventually results. The compound nature of the nucleus of epithelial cells, and of pus-corpuscles after being acted upon by water or dilute acetic acid, is by Henle attributed to the fact of such cells being examined at an early period of their growth, and previous to the complete coalescence of the several particles composing the nucleus.† Henle believes that this mode of development prevails among most elementary cells of the animal body, and he refers, in illustration of it, to the corpuscles of mucus and pus,‡ to those of the lymph and chyle, and to the cells of most glandular structures. With regard to the mode of production of the cell-wall around the nucleus, Henle is of opinion, with other physiologists, that the several elementary granules are so many particles of fat, and that around each one, or a group of them (according as the nucleus happens to be simple or compound) a layer of the albuminous matter of the cytoblastema coagulates and forms a kind of film or coating, in accordance with the fact pointed out by Ascherson,§ that minute globules of oil when brought into contact with liquid albumen, become at once invested by a coherent layer of the albuminous substance, and thus acquire a vesicular character.

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* Allgemeine Anatomie, pp. 152—162.

† Kölliker, as will be presently mentioned, offers a different explanation of this appearance.

‡ Vogel also describes the development of pus in the same way. (Müller's Physiology, p. 466; and Pathologische Anatomie des menschlichen Körpers, 1845, p. 90.)

§ Müller's Archiv, 1840, Ueber die physiolog. Bedeutung der Fettstoffe, &c.

On comparing the above two modes of cell-development with the account furnished by Schwann, it will be observed that there is no striking difference between them; the first plan of development described by Henle agrees essentially with that stated by Schwann, while between Henle's second plan and Schwann's explanation of the origin of the cells containing two (or more) nucleoli, the difference is more apparent than real, and is not in either case founded on direct observation. The chief discrepancy in the accounts of these two observers, appears to consist first in Henle's disinclination to admit the existence and importance of nucleoli, though, as before observed, there is no good reason for regarding the nucleoli as structures dissimilar from Henle's elementary particles or granules; and secondly, in respect of the manner in which the cell-wall is developed around the nucleus.

In Henle's third mode of the development of cells, a large quantity of the elementary granules arrange themselves together into a more or less spherical mass, around which a delicate cell-wall is subsequently formed; but it is not until a later period, if at all, that a nucleus can be perceived in the midst of this mass. Illustrations of this mode of development are presented by the large granular bodies met with in the first milk or colostrum, by the so-called compound inflammation- or exudation-corpuscles, and by many of the globules found in malignant tumours and other morbid products.*

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* It should be remarked, however, that doubts are entertained by several physiologists, of the above being the mode in which the granular exudation-corpuscles found in the products of inflammation, or in other diseased structures, are developed. Vogel (Pathologische Anatomie des menschlichen Körpers, p. 127) is of opinion that these corpuscles are cells which have an origin exactly similar to that described by Schwann, as occurring in the development of other nucleated cells; and he believes that they only subsequently assume the granular condition. Reinhardt (Archiv für pathologische Anatomie und Physiologie, by H. Virchow and B. Reinhardt, 1847,) entertains an almost exactly similar view, and he believes that the exceedingly granular condition of exudation-corpuscles and of other granular-looking cells, is probably always a later change due to the formation of granules of fat, and just precedes the cessation of their period of life, which event is manifested by the disappearance of the nucleus and cell wall, and by the breaking up of the cell into an irregular heap of granules. He believes also, that these retrograde changes take place in cells developed under normal as well as abnormal conditions, and he furnishes many examples in proof of this. The best of these examples is afforded by the changes which ensue in the cells composing the membrana granulosa of the Graafian follicle during the degeneration which the follicle undergoes in the ovary. These cells, in the mature Graafian follicle, are nucleated, and filled with tolerably clear albuminous contents ; but as the follicle degenerates or retrogrades, the cells become opake from the formation of granules or particles of fat among their contents, the nucleus disappears, and ultimately the more or less thick yellowish substance filling the follicle, is found to consist almost entirely of granule cells (like exudation-corpuscles) and heaps of granules, into which the cells have broken up. On the other

Besides these three modes of cell-development, however, Henle recognises, with Schwann and other physiologists, another plan in which simple cells are developed, independent of a pre-existing nucleus; examples of this are seen in the chorda dorsalis of fish and reptiles, as Schwann pointed out, and in cryptogamic and many higher plants, in which a single minute spherule first appears, and this soon becomes a distinct vesicle, rapidly grows, and is eventually extended into a cell.

The results of investigations by Vogt,* on the development of fishes and reptiles, also tend to shew the occurrence of at least three distinct forms in which the development of cells may take place. In one of these forms the cells appear to owe their origin to a pre-existing nucleus, but in the two others they appear to originate independently of a nucleus.

As already stated, Vogt entirely agrees with Henle in his view of the unimportance of the nucleolus in the process of cell-formation. In by far the majority of cells in young Batrachians and fishes nucleoli were entirely absent; and in the few in which they existed, as the cartilage-cells of Batrachians, and the embryonic-cells of the salmon, they appeared to be structures of later formation, occurring as simple vesicles which gradually enlarged into cells apparently at the expense of the nucleus, which by degrees entirely disappeared. In no case did they appear to constitute the first stage in the development of cells out of the cytoblastema in the manner described by Schleiden and Schwann. The *nucleus*, however, appears to be an almost invariable constituent of the cell at whatever period of its life it be examined. But the relation, in point of time, which its development bears to the development of the cell, was found by Vogt, as by Henle and others, to vary in different cases. In one form of cell-development, namely, the production of the cortical cells of the yolk in the toad, the nucleus precedes, and evidently gives rise to, the formation of the cell. In another form, which, as shewn by Henle, is well illustrated in the chorda dorsalis of fish, the cells originate without the intervention of nuclei, which only make their appearance after the cells are fully formed. In the third form, the cell and its nucleus seem to be

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hand, Bruch (Henle and Pfeufer's Zeitschrift, b. iv. p. 50) appears to agree with Henle, for he states that the large granular corpuscles frequently met with in cancerous growths, are formed by an aggregation of granules, within which a nucleus is shortly formed, and the whole then becomes surrounded by a cell-wall. Luschka (Entwickelungs-geschichte der Formbestandtheile des Eiters und der Granulationen. Freiburg. 1845.) also agrees with Henle, in believing that the exudation-corpuscles in inflammatory products are formed by the grouping together of numerous minute granules, around each heap of which a cell-wall is then developed, while a nucleus shortly afterwards makes its appearance in the midst. But he also believes that the corpuscles thus formed constitute only an early stage in the development of pus-corpuscles, into which they are afterwards changed by the absorption of some of their granular matter, and consequent diminution in size.

* Entwickelungs-geschichte der Geburtshelferkröte, 1842, pp. 118—27.

developed coincidently. For, in the embryonic cartilage of the toad, in which this mode of development occurs, Vogt never could detect either free nuclei or cells unprovided with nuclei; when nuclei were found, they were invariably surrounded by a cell-wall, and when cells were found, they invariably enclosed a nucleus. In explanation of this coincident formation of cell-wall and nucleus, Vogt suggests that probably one portion of the granular matter of the cytoblastema, from which a cell is about to be developed, may collect, centripetally, at the centre, to form a nucleus, while another portion may collect around, at some distance from it, by a centrifugal influence, and there form a cell-wall.

Kölliker's * opinion of the mode of origin of cells, founded upon the results of researches on the development of invertebrate animals, differs in several respects from those entertained by Henle and Vogt. For he believes that the so-called primary cell is, as Schleiden and Schwann described, in almost all cases developed around a nucleus, which persists for a greater or less length of time, and that the nucleus also is in most cases formed around a nucleolus. The irregular appearance frequently presented by the nucleus of pus-corpuscles, especially after being acted upon by dilute acetic acid, is not, as Henle supposed, an early character, and an indication of its being originally composed of two or more separate particles—for, at its first formation, the nucleus is invariably a simple vesicular body—but is an after effect, and is due to the nucleus being divided into two or more new vesicular bodies, each of which may, if carefully examined, be seen to contain a minute particle or nucleolus; and these, he thinks, originate by endogenous multiplication.

In a recent essay, H. Müller † has advanced an opinion concerning the development of the corpuscles of pus and of chyle, which differs from that of other writers, and from which it would seem that these corpuscles originate in a manner somewhat similar to the third mode of development described by Vogt. He believes that previous to the development of cells the chyle consists of a number of particles, some of which are soluble, others insoluble. In the production of chyle-corpuscles or cells, a number of both kinds of particles become aggregated into a mass; shortly after the formation of which, the insoluble particles collect together in the centre to form the nucleus, while the soluble ones dispose themselves around the circumference, and are transformed into the cell-wall. A very similar process he states to be pursued in the formation of pus-corpuscles.

Such are some of the principal observations which have been lately made on the subject of the development of cells. The amount might have been considerably extended by including the remarks of many other

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* Entwickelungs-geschichte der Cephalopoden, 1844, p. 142.

† Beiträge zur Morphologie des Chylus und Eiters, in Henle und Pfeufer's Zeitschrift, b. iii.

writers on the subject, but since these have, for the most part, a tendency to confirm one or other of the views stated above, it is perhaps unnecessary to do more than refer to them here.* In collecting together the above facts, it has been the writer's endeavour to ascertain whether the various accounts of different observers could be so far reconciled as to furnish conclusions pointing to the existence of any one uniform and constant plan, according to which the development of cells is in all cases effected. But it will be at once evident, from what has been stated above, that so far as our present data extend, no such single uniform plan can be said to exist; though it is not improbable that further investigations will shortly lead to its discovery, and that then the several varieties hitherto observed, may be found to be only modifications of one universal mode of development.

From what has been said above, it appears tolerably certain that cells may sometimes originate independent of pre-existing nuclei, and that, therefore, the views of Schleiden and Schwann in respect of the importance of these structures in the genesis of cells, must be somewhat modified. Yet it is not satisfactorily shewn that in any mode of cell-formation cases ever occur in which one or more minute elementary particles, corresponding to the nucleoli of Schwann, do not exist previous to the formation of any other part of the cell. If subsequent investigations prove that the pre-existence of such particles is a circumstance of invariable occurrence, it may be reasonably inferred that they are the real germs or cytoblasts from which the cells originate. When once formed, these particles may give rise to the production of cells in one or other of the various ways above described. Each one may either grow and be itself developed into a cell by incorporating nutritive matter, and simply enlarging, as is supposed by Mr. Macleod † to be the case in the development of the blood-corpuscles of the chick, by Vogt ‡ in the development of the cells of the chorda dorsalis, and by Karsten § in the development of all varieties of cells. Or it may serve as a centre around which matter is deposited to form a nucleus, from which a cell-membrane subsequently springs in the manner maintained by Schleiden and Schwann to prevail in most vegetable and animal tissues. Or, again, it may serve as the true nucleus to a primary cell growing around it; and this, by Kölliker, is considered to be its ordinary office. It must be mentioned, also, that even a primary cell may act the part of a nucleus, so far, at least, as to cause the growth around it of another secondary cell-membrane.

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* The whole subject will be found well discussed by Reichert, in his Reports in Müller's Archiv. during the last three or four years, by Kölliker in Schleiden and Naegeli's Zeitschrift, and by Henle in his late Reports in Canstatt's Jahresbericht.

† London and Edinburgh Monthly Journal of Medical Science, Sept. 1842.

‡ Entwickelungs-geschichte der Geburtshelferkröte, p. 126.

§ De Cellâ Vitali. Berlin, 1843.

Examples of this are furnished by the ganglion-corpuscles of nerve-substance, and by the ovum. Kölliker, indeed, considers that all ordinary nucleated cells should be regarded in the light of secondary or complex cells.

3. From the several details which have just been considered in relation to the development of cells, it would appear that in the cytoblastema there resides some power by which fresh cells can be continually formed out of an apparently homogeneous fluid. In order that this continual formation of successive crops of cells may be effected, it is essential, however, that constant supplies of new formative fluid should be provided, and it appears to be one of the purposes served by cells, to elaborate this fresh formative material, which, when perfected, is discharged by the solution of the membranous cell-walls. Out of the fresh cytoblastema thus prepared and liberated, the new cells are developed in one or other of the ways above pointed out. And it would seem, as stated by Schwann, that, in the case of animal structures, the continued increase of cells, is in most cases, effected by such fresh development in the free formative fluid. But in several other cases new cells are formed within the cells of a preceding generation, and by these they are surrounded until they have attained a certain degree of development, when they escape, apparently by rupturing the parent cell which then disappears. This *endogenous* mode of cell-formation, (or *multiplication*, as it is commonly termed,) although of common occurrence among vegetable structures, is, however, comparatively rare in animals; the ovum, cartilage, and a few other structures presenting the only known examples of it. It differs from the original development of cells in the circumstance of the new cells being produced more or less directly from some part of a pre-existing cell, which thus acts as a kind of re-productive organ. But it is not improbable that the difference is one more apparent than real, and consists simply in the circumstance of the source whence the new cells originate, being in the one case retained within the parent-cell, and in the other case set free.

The best examples of the endogenous mode of cell-multiplication have been already mentioned in describing the changes which ensue in the development of the ovum.* It was there shewn (in the case of the ovum of Cucullanus elegans) that according to Kölliker's observation the first step in the process of multiplication consists in the nucleus of the first cell which is formed after the disappearance of the germinal vesicle, becoming constricted in the middle, and subsequently dividing into two equal halves, each of which serves as a separate nucleus, around which a new cell forms; and each new cell in its turn gives rise to two others formed in the same way, and so the process goes on until the whole mass of the ovum is made up of such cells. And Kölliker appears to be of opinion that in most other cases of cell-multiplication the division of the nucleus is the first essential step in the process.† Other cases, however, seem to occur in which the nucleus, instead of dividing into two portions, only breaks up into several particles (though even this may be effected by successive duplications) each of which appears to possess the power of enlarging and becoming vesicular; the several minute vesicles as they increase in size gradually obliterating the original nucleus, and eventually constituting the chief contents of the cell. Each of these minute vesicular particles probably constitutes a germ of a fresh cell, into which it is subsequently developed either by simple enlargement, or by serving as a cytoblast around which a cell-wall forms. In other cases, again, apparently under the influence of the nucleus when present, or even independent of it, minute vesicular bodies are developed within the cell itself, which by enlarging they gradually fill, and eventually burst. Previous to their discharge from the parent cell, or shortly afterwards, a new generation of cells is developed within each of them by the same process by which they themselves had been formed. Another form of cell-multiplication has been described as occurring in vegetable structures, in which a cell appears to divide by the formation of a partition across its cavity, whereby two new cells are formed. But as explained by Schleiden, in which explanation Dr. Sharpey* agrees, this apparent mode of division is probably merely an instance of the endogenous production of twin cells, the contiguous sides of which form the septum as in C, fig. 8, p. 71. In a few cases, again, the multiplication of cells takes place by the growth of young sprouts or offshoots from the parent cell. This variety, which is confined entirely to vegetable structures, is well illustrated in the mode of growth of the yeast-plant.†

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* See especially p. 66 and p. 71.

† Entwickelungs-gesch. der Cephalopoden, p. 150.

4. The tendency of nearly all recent observations on the subject has been to confirm the general correctness of Schwann's account of the various *changes which the primary cells undergo in the production of the elementary tissues* of the body.‡ In some instances, however, there is sufficient evidence to shew that this account requires to be modified. This seems to be especially the case in regard to the cellular, tendinous, and elastic tissues, each of which was supposed by Schwann to be formed by the elongation of cells and their division into bundles of fibres. But that such a mode of development appears not to take place will be presently shewn when considering the transformations undergone by the nuclei.

In regard to the development of bone, a considerable amount of information has been of late added to the comparatively imperfect account of it furnished by Schwann. But it is considered unnecessary to enter here into the details of this, since the whole of the subject has been of late so ably discussed by Dr. Sharpey, in a standard work on anatomy.§

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* Quain's Anatomy. Fifth edition, p. xlviii.

† For accounts of the above modes of cell-multiplication see especially Henle, Kölliker, Vogt, Reichert, and Vogel, in the works referred to.

‡ For this account see Müller's Physiology, pp. 397 and 1643.

§ Quain's Anatomy, by Dr. Sharpey and Mr. Quain, p. cxlvii.

Several new facts have also been added concerning the development of nerves, which tend to throw fresh light on the physiology of the nervous system, since they render it almost certain that the central terminations (or origin) of nerve-fibres are not disposed in loops, as until lately has been generally supposed to be the case, but that they pass directly into the nerve-corpuscles which compose so large a portion of the grey substance of nervous centres. Both Müller and Remak, several years ago, observed that from some of the corpuscles of the grey substance of the brain, spinal cord, and ganglia, fine tooth-like processes issue, and may be sometimes traced to the extent of many times the diameter of the corpuscles.* The resemblance which these processes bear to the delicate, grey filaments observed by Remak in the sympathetic nerves, led to the suggestion that the two are identical, and that the latter filaments take their origin directly from the ganglion corpuscles. These observations, however, do not appear to have attracted much further notice; but it has been found by more recent investigations, that Remak's suggestion concerning the origin of sympathetic nerve-fibres is perfectly correct, and moreover that the fibres of the cerebro-spinal nerves also have, as was indicated by Ehrenberg,† an exactly similar origin.‡ Without entering into the details of these important investigations, the consideration of which would be foreign to the present purpose, it may be remarked that in the junction of the nerve-fibres with the ganglion-corpuscles, the contents of the central part of the fibre (the axis-cylinder of Purkinje and Rosenthal, the primitive band of Remak) pass directly into the granular contents of the corpuscle, while the fine external sheath of the nerve-fibre becomes continuous with the membranous envelope, within which the granular substance of the corpuscle is contained. The phenomena observed during the development of nerve-fibres in the embryo, especially by Schaffner§ and Kölliker,‖ agree very closely with these facts. In the earliest period of its formation nerve-substance consists almost entirely of roundish, mostly nucleated cells filled with a finely granular material, and, with the exception of being somewhat smaller, exactly similar to the nerve-corpuscles found in the nervous centres of the adult animal. As the development proceeds, but previous to the appearance of distinct nerve-fibres, many of these cells send forth fine tubular processes of an apparently homogeneous structure, which unite with similar processes from other cells, and thus, in time, give rise to continuous nerve-tubules. Kölliker finds that in young

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* Müller's Physiology, vol. i. p. 657.

† Structur des Seelenorgans. Berlin, 1836.

‡ See Helmholtz, de Fabric. System. Nerv. evertebratorum. 1842; Kölliker, die Selbstand. und Abhang. des sympath. nervensyst. Zurich, 1844; Dr. Will, in Müller's Archiv. 1844; Dr. Todd and Mr. Bowman, Physiological Anatomy of Man, vol. i. p. 213; and more especially R. Wagner, Neue untersuchungen über den Bau und die endigung der Nerven und die Struktur der Ganglien, Leipzig, 1847, and Dr. F. H. Bidder, zur Lehre von dem Nervenfasern. Leipsig, 1847.

§ Schmidt's Jahrbücher, 1847.

‖ An. des Sc. Nat. Zoologie, 1846, p. 104.

Batrachians, a complete network of nerve-tubes is formed by this junction and coalescence of the processes from branching cells: a similar observation was also made by Schwann.* According to Schaffner, as the nerve-tubules coalesce and increase in size, the walls of the cells from which they originate are gradually drawn out and merge into those of the tubules, while their granular contents also become continuous and identified with the contents of the tubules.

In considering the transformation which cells undergo in the development of tissues, too much stress cannot be laid on the importance of the share taken by the nuclei in these changes, especially since this appears to have been entirely overlooked by Schwann. It is proposed, therefore, to bring together some of the more striking circumstances which seem to demonstrate the importance of nuclei, whether considered as individual structures, or as component parts of cells. That the nuclei may exist in tissues apparently independent of cells, has been shewn especially by the observations of Mr. Paget,† who found that many morbid growths are composed almost entirely of corpuscles like nuclei or cytoblasts. These morbid structures were usually tumours of very rapid growth, and from the almost invariable presence of large quantities of nuclei, it would seem that they must play an important, if not the chief part in this growth. The abundance of nuclei in most, if not all, other actively growing tissues, healthy as well as morbid, their persistence in those tissues, such as the muscular, in which a constant waste and repair consequent on the active discharge of their function is taking place, their invariable existence in the secreting cells of all glands and epithelia, and their disappearance from the cells of fat, which when fully formed cease to perform any active function, all attest the importance of the share taken by the nuclei in the processes of growth, reproduction, and secretion. Equally strong confirmation of this is furnished also by the variety of examples in which development, in either structure or composition, is effected in the animal organism by cells unprovided with nuclei, while there are many instances in which nuclei, whether contained in cells or without them, appear to assume higher forms, or to be centres and sources of formative and reproductive power.‡ The evidence of these facts is based chiefly on his own observations on tumours above alluded to, and on the investigations of Professors Henle § and Goodsir,‖ and of Mr. Simon.¶ The researches of the last-named observer on the glands without ducts, tend to prove the discharge of a large amount of gland-function by nuclei alone; for in the thymus, the splen, and other such glandular organs, minute vesicular bodies, in all respects similar to nuclei or cytoblasts, exist in considerable abundance, and appear to be the essential parts concerned in discharging the functions of these organs. And Professor Goodsir's observations in several of his papers * seem to demonstrate the power of the nucleus both in the production and multiplication of cells, and in the formation and storing of secretions.

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* Mikroscopische Untersuchungen, p. 177.

† Report on Anatomy and Physiology for 1844–5, p. 35.

‡ Mr. Paget, Lectures at the Royal College of Surgeons, May 1847. Lecture 5.

§ Allg. Anat. pp. 192—9.

‖ Anatomical and Pathological Observations, 1845.

¶ A Physiological Essay on the Thymus Gland, 1845.

The transformation of nuclei into higher tissues has been shewn especially by the researches of Henle,† and more recently by those of Kölliker.‡ According to Schwann's system of cell-formation, the nucleus is supposed to disappear shortly after the perfect state of the cell is attained. But the results of recent observations have shewn that the disappearance of the nucleus is of much more rare occurrence than was supposed by Schwann to be the case, and, moreover, that instead of disappearing, the nucleus in many cases assumes a higher degree of development, and is transformed into a more or less persistent tissue. According to Henle,§ the only parts in which the nucleus disappears are the blood-corpuscles, the cells of the epidermis and the nails, and most of the fat-cells, the tubules of the crystalline lens and of enamel, and many of the cartilage-corpuscles. But in all fibres supposed to be formed from coalescing cells (except those of the lens and enamel), the nuclei remain, and, moreover, undergo remarkable transformations. For example, they assume an oval shape, then gradually elongating and becoming narrow, are converted into fine dark streaks, which lie in straight, angular, tortuous, or spiral lines upon the fibres. After being thus changed they either gradually disappear, or becoming more elongated and meeting with each other, they unite to form a new set of fibres, which, from their mode of origin, he calls nucleus-fibres. Occasionally these nucleus-fibres send off lateral branches, by which a kind of continuous network is formed over the surface of each layer of the tissue in which this arrangement occurs. Various other modes of arrangement of these nucleus-fibres are observed in different tissues. The fibres are remarkable for their dark well-defined outline, and being insoluble, like other nuclei, in acetic acid, their existence and peculiarity in a tissue may be at once ascertained by means of this re-agent. Ordinary elastic tissue appears, according to Henle,‖ to be only a variety of such nucleus-fibres.

Another remarkable purpose served by nuclei in the formation of tissues has been pointed out by Henle as seen especially in the coats of blood-vessels. In the development of these coats, layer after layer of cytoblastema is deposited in the form of structureless membrane, and in each of these, nuclei are shortly formed and undergo several different changes. In the innermost layer cells grow around the nuclei, and thus is formed the

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* Op. cit. articles "Centres of Nutrition," "Secreting Structures," and "Serous Membranes." † Allg. Anat. pp. 192—9. ‡ Entwickelungs-ges. der Cephalopoden, p. 145.
§ Allg. Anat. p. 192. ‖ Allgemeine Anatomie, p. 407.

epithelial coat of the vessel. In the next layer, which forms the so-called internal coat of the vessel, the nuclei remain unaltered. But in the formation of the muscular or contractile coat of arteries, the nuclei elongate and arrange themselves in rows in the manner before described. Moreover each row of elongated nuclei appears to appropriate the adjoining strip of structureless membrane in which it is imbedded, and the result is that this membrane breaks up into a number of flat fibres, each bearing upon its surface the row of nuclei after which it was modelled. Organic muscular fibres of other parts of the body are formed after exactly the same plan. In the formation, also, of fibro-cellular or areolar tissue, the nuclei are arranged in rows, to each of which is appropriated a strip of the cytoblastema; and each such strip, instead of remaining flat and ribbon-like, as is the case in organic muscular fibre, breaks up into a bundle of parallel longitudinal fibrillæ. This is quite opposed to the account given by Schwann* of the development of fibro-cellular tissue. Kölliker,† in alluding to these several transformations undergone by the nuclei, mentions also, as other instances, the different modes of development of seminal filaments directly from nuclei,‡ and the growth of the spines of several invertebrate animals.

Arguments in favour of the view of the importance of the nuclei to the growth and well-being of the tissues in which they occur, are furnished also by the phenomena which attend their retrograde, as well as their advancing transformations—their degradation as well as their development. For it has been rendered highly probable by the investigations of Mr. Paget,§ that in all cases of atrophy accompanied with degeneration of tissue, the nuclei of the degenerated part lose their characteristic properties, or entirely disappear. This is especially the case in fatty degeneration (or atrophy) of muscle, of the liver and of the kidney, in all well-marked instances of which, the nuclei, of the fibres in one case, of the hepatic and renal cells in the other cases, have completely disappeared, their place being occupied with fat, in the form of granular matter, or drops of oil.

Development of the Blood.

It may be desirable here to present some account of the principal observations recently made on the development of the blood corpuscles. Concerning the original formation of these corpuscles in the embryo, the results of nearly all recent investigations tend to shew that, as was stated by Reichert,‖ at the first appearance of a vascular system they consist, in all vertebrate animals, of nucleated, colourless, granulated cells, identical with the formative, vitelline, or embryonic cells of which all the structures of the embryo are originally composed; that they are, in fact, the central cells of the solid mass of which the heart and large blood-vessels at first consist. A difference of opinion, however, still exists with respect to the mode in which these original cells are converted into the characteristic corpuscles subsequently found in the blood.

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* Müller's Physiology, p. 1646, and fig. 253.

† Entwickelungs-gesch. der Cephalopoden, p. 145.

‡ For an account of these modes of development, see p. 41.

§ Lectures at the Royal College of Surgeons, May, 1847. Lecture V.

‖ Müller's Physiology, p. 1550.

According to Vogt, from observations made on the larva of the toad,[†] (Alytes obstetricans,) and on the embryo of the salmon (Coregonus palæa[‡]), the cell-wall of each original cell gradually disappears, and the liberated nucleus, in which a secondary nucleus is subsequently formed, becomes the true nucleated blood-corpuscle. The circumstances which he urges in favour of this view are, first, the close correspondence in size between the nuclei of the original cells and the true corpuscles of the blood; and, secondly, the non-existence of a nucleus at first in the small corpuscles, and its appearance subsequently. Against this view it is objected, by MM. Prevost and Lebert,[§] from observations also made on Batrachians, that there is by no means so close a resemblance in size between the nuclei of the primitive cells and the corpuscles of the blood, as stated by Vogt, but that the size of the latter more nearly corresponds with that of the cells themselves: and that, contrary to Vogt's statement, a nucleus may be detected in the blood-corpuscle in all the phases of its evolution. According to these observers, the blood-corpuscles result from a direct transformation of the cells themselves, which assume an ellipsoid instead of their previously round form, become flattened, lose their granular matter, and acquire coloured contents. Kölliker, also, is opposed to the account given by Vogt, and is of opinion with Prevost and Lebert, that in Batrachians, and also in Mammalia, the embryonic cells themselves are directly transformed into the true blood-corpuscles. Like Prevost and Lebert, he also was unable to find non-nucleated corpuscles in the blood of larval frogs, and of the earliest embryos of Mammalia. A similar view to that of the last three named observers concerning the direct origin of the earliest blood-corpuscles from the embryonic cells, appears to be entertained also by most other physiologists.[¶]

The conversion of embryonic cells into true blood-corpuscles, in whatever way effected, is probably completed very shortly after the formation of a cavity in the heart and in the large blood-vessels in connection with

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[*] Entwickelungs-geschichte der Gebürtshelferkröte, p. 70.

[†] In Agassiz's Hist. Nat. des Poissons d'eau douce, tome i. p. 203.

[‡] An. des Sc. Nat. 1844, p. 212.

[§] An des Sciences. Nat. 1846, p. 43.

[||] Mr. Macleod (London and Edinb. Monthly Journ. of Med. Sc. Sept. 1842,) is of opinion, however, that in the chick the earliest blood corpuscles are developed from minute dark spherical granules of which alone the blood at first is composed. He believes that each of these possesses the power of enlarging, and being developed into a circular nucleated cell, which subsequently flattens, assumes colouring matter, grows oval, and thus becomes a true red blood-corpuscle.

this organ, and after this period their share in the production of blood-corpuscles appears to cease. The next point, therefore, to be considered, is the mode in which the subsequent multiplication of the corpuscles thus formed is effected. According to Kölliker,* this multiplication in the earliest period of embryonic life takes place, in Mammalia, either by the actual division of each coloured nucleated corpuscle into two or more secondary corpuscles, the number of which is determined by the number of nuclei developed in the corpuscle previous to its division, and which seldom exceeds two, though it occasionally amounts to three, or, as figured by Fahrner,† even to four; or, secondly, by the formation of two or three smaller corpuscles within each large one, which subsequently dissolves away and liberates its brood. Whichever of these modes of multiplication is pursued, he considers, however, that it is brought to a complete close so soon as the liver is developed. Then, in his opinion, the production of blood-corpuscles is due entirely to this organ, by whose agency an abundant formation of nucleated colourless corpuscles is soon effected, and continues to take place probably through the whole period of embryonic life. The colourless corpuscles thus formed, which are quite different from the colourless embryonic cells found at the first development of the blood, are in all probability converted into coloured blood-corpuscles, either at once, or not until they have multiplied in one or other of the modes just described as happening to the first formed coloured corpuscles. Of the coloured nucleated corpuscles which result from such transformation, the majority flatten, lose their nuclei, and shortly assume all the characters of the ordinary coloured non-nucleated corpuscles found in the blood of Mammalia. The relative quantity of these latter corpuscles increases in proportion to the age of the embryo, so that they soon constitute the principal element of the blood, except of that of the liver, in which, at all periods of embryonic life, colourless and coloured nucleated corpuscles occur in great abundance, owing apparently to the activity of the process of blood-development there taking place.

The latter part, at least, of this account of Kölliker, was fully confirmed by the results of observations made by Mr. Paget, Mr. Malden, and the writer. In a sheep's embryo about four inches and a quarter in length, while the blood of the rest of the body consisted almost entirely of ordinary red non-nucleated corpuscles, that from the liver (obtained from a clot drawn from a section of this organ) contained, besides dark red corpuscles, a large quantity of different-sized, pale, granular, and largely nucleated cells, the characters of which were quite distinct from those of the ordinary liver-cells. Still stronger evidence in favour of this view was obtained from the examination of the blood of a human fœtus at about the commencement of the fifth month of pregnancy. For, while the blood from the left ventricle of the heart, from the umbilical artery and vena cava superior, was composed principally of ordinary red non-nucleated corpuscles, with a very few pale granular cells, that from the liver and that also—though from this source the characters of the blood were less manifest—from the vena cava inferior just previous to its entrance into the right auricle, contained, besides red non-nucleated corpuscles, a considerable number of ordinary pale corpuscles like lymph-corpuscles, and several larger pale granular corpuscles, with distinct large nuclei. The appearances, indeed, presented by the blood obtained from these two latter sources, but especially from the liver, were just such as would indicate the existence of a process of rapid development of blood-corpuscles. Of this process the several varieties of corpuscles found, probably represented so many stages from the first condition of pale spherical granular nucleated cells, to the coloured, flattened, smooth, non-nucleated corpuscles.*

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* Henle und Pfeufer's Zeitschrift, 1846, p. 112, *et seq.*

† De Globulorum Sanguin. in Mammal. Embryon. et adultis origine. Inaug. Diss. 1845.

With regard to the probable mode in which the liver performs this office of developing blood-corpuscles, Kölliker does not offer any decided opinion. He considers that it bears no particular relation to the development of the proper secreting tissue of the organ, for the formation of blood-corpuscles in the liver takes place even before the secretion of bile commences. Professor E. H. Weber,† who also admits the importance of the liver as an organ for the formation of blood in the embryo, at least of birds and frogs, is of opinion that the elements of bile and the corpuscles of blood stand, as it were, in a kind of complemental relation to each other, the separation of the one furnishing the conditions favourable to the development of the other. The seat of formation, however, both of the blood corpuscles and the bile is considered by Weber to be in the network of minute biliary ducts, and not in the blood-vessels. Certain materials (the contents of the yolk-sac in early embryonic life) are abstracted from the latter into the former set of vessels; and from these materials are formed the elements of bile, and the corpuscles of blood: the one are conveyed through the bile ducts to the gall-bladder and intestines, the others make their way into the blood-vessels; but in what manner is by no means clear.

Whatever share may be taken by the liver in the production of blood-corpuscles during embryonic life, the results of the most recent observations on the subject of the development of the blood, especially of those furnished by Kölliker,‡ Mr. Wharton Jones,§ and Fahrner,‖ to the general truth of which the testimony of the writer, from observations above alluded to, may be added, have shewn that, in the blood of the early Mammalian embryo, at least three several kinds of corpuscles are met with.

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* And, since the above was written, still further confirmation of the truth of such an opinion has been obtained from additional examinations of the blood of other Mammalian embryos at different ages.

† Henle und Pfeufer's Zeitschrift, l. c. p. 161.

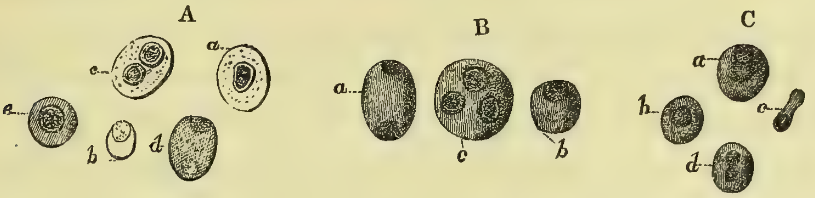
‡ Op. cit.

§ Philosophical Transactions, 1846.

‖ Op. cit.

These are—to enumerate them by the terms adopted by Kölliker, and to place them in the probable order of their development—1. colourless nucleated corpuscles (fig. 25 A); 2. coloured nucleated corpuscles (B and C); and 3. coloured non-nucleated corpuscles. Varieties in size, form, relative numbers, and shades of colour, are observed in these corpuscles, such as might be expected from the circumstance that they are probably only different transitional stages of development of one kind of corpuscle, and that bodies in all the intermediate states of this transition are commonly met with in the same sample of blood. Without describing these varieties, which may be found detailed at length by Mr. Wharton Jones, and by Kölliker—with whose descriptions the observations of the writer for the most part agree—it will be sufficient to observe here that very little doubt now remains of the correctness of the opinion that the first variety, namely, the pale or colourless nucleated corpuscles (which, according to Kölliker, are developed in the liver) constitute an early stage in the development of the perfect red corpuscles, and that they are gradually transformed, first into the nucleated coloured corpuscles, by assuming colouring matter, and then into the non-nucleated coloured ones, by losing their nucleus and becoming flattened.

Fig. 25.*



The mode in which the nucleus disappears is not clearly determined. Mr. Wharton Jones is of opinion that the nucleus escapes from the cell, and becoming coloured, constitutes the ordinary red non-nucleated corpuscle of mammalian blood. The principal circumstance which he urges in favour of this view is, that, at least in the adult animal, there is an almost exact correspondence in size between the nucleus of the nucleated blood-cell and the non-nucleated red corpuscle; and that in those animals which have small red corpuscles, as the goat, the nucleus of the nucleated cell also is small, whilst in those which have large red corpuscles, as the elephant, the nucleus also is large.

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* Fig. 25. Blood corpuscles from a three months' human embryo, magnif. 300 diams. After Kölliker. A. Nucleated colourless corpuscles from the blood of the liver. *a*, a large nucleated corpuscle with a clear fluid and granules in its interior; *b*, a smaller one from which the granules have disappeared; *c*, a pale double-nucleated corpuscle with granules; *d*, a double-nucleated one slightly coloured; *e*, a single-nucleated, slightly coloured corpuscle, from which the granules have disappeared. B. Slightly coloured nucleated blood-corpuscles from the liver; *a*, with two; *b*, with one; c, with three nuclei. C. Dark-coloured nucleated blood-corpuscles from the aorta; *a*, a large one, with a slight depression; *b*, a smaller one; *c*, one viewed laterally; *d*, a smaller one with a constricted nucleus.

The preponderance of nucleated coloured corpuscles in the blood of the very early mammalian embryo, and their gradual diminution in quantity as the fœtus increases in age was noticed by Kölliker. In other observations which the writer made with Mr. Paget on the blood of two embryonic sheep, each about seven lines in length, the truth of this remark was fully confirmed, as also of the fact observed by other physiologists that the blood corpuscles of the fœtus are decidedly larger than those of the adult. In the blood of each of the embryonic sheep by far the majority of the corpuscles were coloured, had a diameter at least twice as large as that of the red corpuscles in the uterine vein of the parent, and were biconvex in form, often somewhat distorted, and Saturn-shaped; the addition of water brought into view nuclei in almost all of them.*

With regard to the development or fresh formation of corpuscles in the blood after the cessation of embryonic life, Kölliker favours the view advocated by the translator of Müller's Physiology,† and adopted by many physiologists, that this is effected by the transformation of the pale corpuscles of the blood, which (developed in the liver during embryonic life, after this period) are identical with the corpuscles found in the lymph and chyle. In this transformation the corpuscles possibly pass through transitional stages somewhat similar to those undergone by the pale corpuscles of the embryonic blood, though, if this be so, the whole process must take place most rapidly, for the occurrence of the stage of coloured nucleated corpuscle is one of extreme rarity, and has never been observed in the blood of the human subject. Mr. Wharton Jones states that he has seen it in the blood of the horse, and of the elephant. Dr. Carpenter,‡ however, and some other physiologists are still of opinion that the red corpuscles do not owe their origin to the pale ones, but that they multiply either by the division of each corpuscle into two, as maintained by Dr. Owen Rees,§ or by its breaking up into six or more segments, each of which becomes a young blood-disc, as described by Dr. Barry.||

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* Subsequent examinations of the blood of several embryonic sheep of various sizes with the particulars of which the writer has been kindly furnished by Mr. Paget, would seem to prove a constant resemblance, except in form, between the characters of Mammalian blood at all periods of embryonic life before the disappearance of the branchial fissures, and those of the blood of fish, in which animals the branchial apparatus is persistent. And it would appear that those peculiarities which characterize the blood of Mammalian animals during extra-uterine life are assumed by the fœtus at the time of, or just after, the closure of the branchial fissures.

† Vol. i. page 155.

‡ Principles of Human Physiology, third edition, p. 107.

§ Gulstonian Lectures, Medical Gazette, March, 1845.

|| Phil. Trans. 1840.

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ERRATA.

PAGE

52. The title of M. Zwicky's dissertation on the corpus luteum, which has been accidentally omitted, is "De Corporum Luteorum Origine atque Transformatione. Diss. Inaug. by H. L. Zwicky, Turici, 1844."

99, 8 lines from the bottom, *instead* of "M. Dumesny," *read* "M. Duvernoy;" and in the *note* corresponding to this, *after* "1844," *read* "Zoologie, tome i."

112, *note, after* "Menschlichen," *read* "Körpers."

125, 11 lines from the bottom, *instead* of "variety," *read* "rarity."

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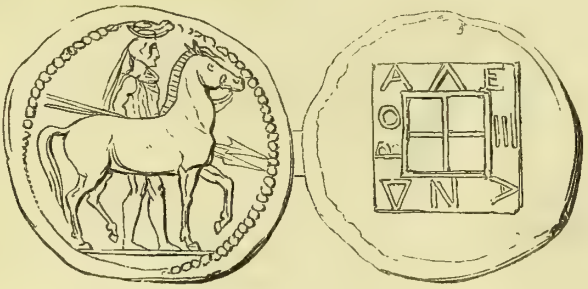

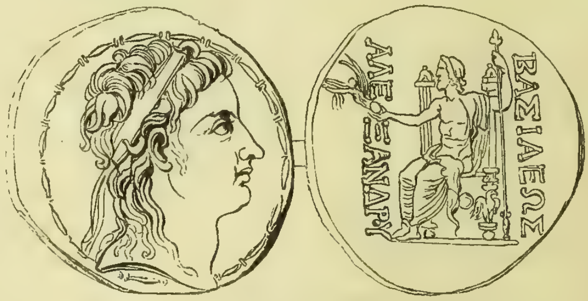

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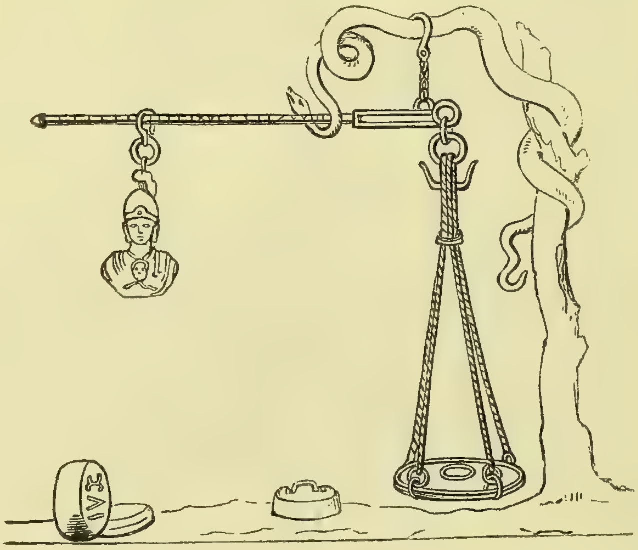

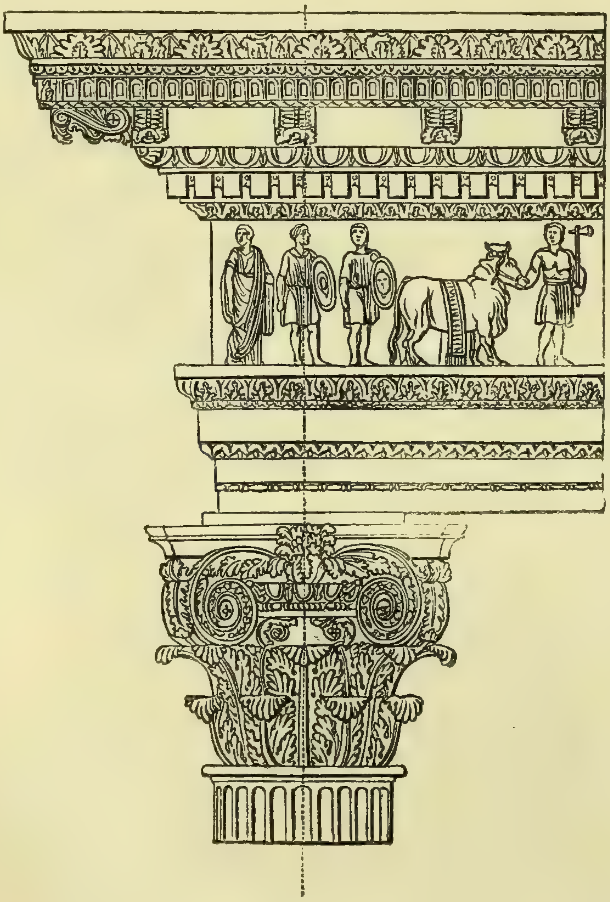

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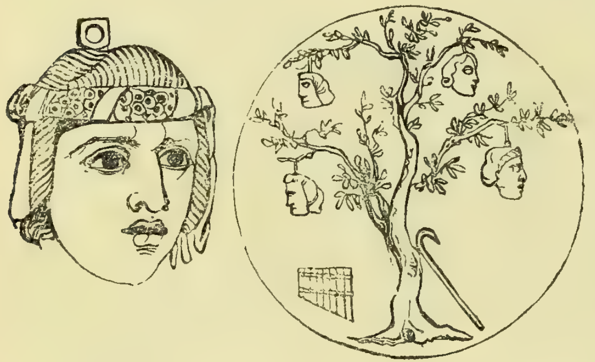
viz. wine, honey, cheese, flour, and a little oil. (Athen. xi. p. 495.) According to other accounts the victor only drank from this cup. The story which was symbolically represented in the rites and ceremonies of this festival, and which was said to have given rise to it, is related by Plutarch (*Thes.* 22, 23) and by Proclus (p. 388, ed. Gaisford). (Compare Bekker's *Anecdot.* p. 318 ; Etymol. Magn. and Hesych. *s. v.* Ὦσχοι ; Suidas, *s. v.* Ὠσχοφόρια and ὠσχοφόρος.) [L. S.]

OSCILLUM, a diminutive through *osculum* from *os*, meaning "a little face," was the term applied to faces or heads of Bacchus, which were suspended in the vineyards to be turned in every direction by the wind. Whichsoever way they looked, they were supposed to make the vines in that quarter fruitful. (Virg. *Georg.* ii. 388—392.) The left-hand figure in the annexed woodcut is taken from an oscillum of white marble in the British Museum. The back of the head is wanting, and it is concave within. The mouth and pupils of the eyes are perforated. It represents the countenance of Bacchus with a beautiful, mild, and propitious expression (*molle*, *honestum*, Virg. *l. c.*). A fillet, spirally twisted about a kind of wreath, surrounds the head, and descends by the ears towards the neck. The metallic ring, by which the marble was suspended, still remains. The other figure is from an ancient gem (Maffei, *Gem. Ant.* iii. 64), representing a tree with four oscilla hung upon its branches. A SYRINX and a PEDUM are placed at the root of the tree.



From this noun came the verb *oscillo*, meaning "to swing." Swinging (*oscillatio*) was among the bodily exercises practised by the Romans, and was one of the amusements at the Feriae Latinae. (Festus, *s. v.* ; Hygin. *Fab.* 130 ; Wunder, *Comment. ad Cic. pro Planc.* p. 93 ; FERIAE, p. 530, a.] [J. Y.]

O'SCINES. [AUGUR, p. 175, b.]

OSTIA'RIUM was a tax upon the doors of houses, which was probably imposed along with the *Columnarium* by the *lex sumtuaria* of Julius Caesar. It was levied by Metellus Scipio in Syria, together with the Columnarium, on which see COLUMNARIUM (Caes. *B. C.* iii. 32 ; Cic. *ad Fam.* iii. 8).

OSTIA'RIUS. [DOMUS, p. 427, b.]

O'STIUM. [JANUA.]

OSTRACISMUS. [EXSILIUM, p. 514.]

O'STRACON (ὄστρακον). [FICTILE.]

OVA'TIO, a lesser triumph, ; the terms employed by the Greek writers on Roman history are εὔα, εὐαστής, πεζὸς ϑρίαμϐος. The circumstances by which it was distinguished from the more imposing solemnity [TRIUMPHUS] were the following: — The general did not enter the city in a chariot drawn by four horses, but on foot ; he was not arrayed in the gorgeous gold embroidered robe, but in the simple toga praetexta of a magistrate ; his brows were encircled with a wreath not of laurel but of myrtle ; he bore no sceptre in his hand ; the procession was not heralded by trumpets, headed by the senate and thronged with victorious troops, but was enlivened by a crowd of flute-players, attended chiefly by knights and plebeians, frequently without soldiers ; the ceremonies were concluded by the sacrifice not of a bull but of a sheep. (Plut. *Marcell.* c. 22 ; Dionys. v. 47 ; Gell. v. 6 ; Liv. iii. 10, xxvi. 21.) The word *ovatio* seems clearly to be derived from the kind of victim offered, and we need pay little respect to the opinion of Festus (*s. v. Ovantes*), who supposes it to have been formed from the glad shout O ! O ! frequently reiterated, nor to that of Dionysius, whose system required him to trace every custom to a Grecian origin, and who therefore maintains that it is corrupted from the Bacchanalian εὔοι. Dionysius makes another mistake in assigning a laurel chaplet to the conqueror on these occasions, since all the Roman writers agree with Plutarch in representing that the myrtle crown, hence called *Ovalis Corona*, was a characteristic of the ovation. (Festus, *s. v. Ovalis Corona ;* Plin. *H. N.* xv. 29 ; Plut. ; Gell. *ll. cc.*) Compare CORONA, p. 361.

In later times, the victor entered upon horseback (Serv. *in Virg. Aen.* iv. 543), and the ovations celebrated by Octavianus, Drusus, Tiberius, &c., are usually recorded by Dion Cassius by a reference to this circumstance. (Dion Cass. xlviii. 31, xlix. 15, liv. 8, 33, lv. 2.)

An ovation was granted when the advantage gained, although considerable, was not sufficient to constitute a legitimate claim to the higher distinction of a triumph, or when the victory had been achieved with little bloodshed, as in the case of Postumius Tubertus, who first received this honour (Plin. *H. N.* xv. 29) ; or when hostilities had not been regularly proclaimed (Festus, Gell. *ll. cc.*) ; or when the war had not been completely terminated, which was one of the ostensible reasons for refusing a triumph to Marcellus on his return from Sicily (Plut. *l. c. ;* Liv. xxvi. 21) ; or when the contest had been carried on against base and unworthy foes, and hence when the servile bands of Athenion and Spartacus were destroyed by Perperna and Crassus, these leaders celebrated ovations only (Florus, iii. 19 ; Plin. Gell. *l. c.*), although the latter by a special resolution of the senate was permitted to wear a laurel crown. [W.R.]

OVI'LE. [COMITIA, p. 336, b.]

OU'SIAS DIKE. [ENOIKIOU DIKE.]

OXYBAPHUM. [ACETABULUM.]

P.

PA'CTIO, PACTUM. [OBLIGATIONES.]

PAEAN (παιήων, παιάν, παιών), a hymn or song which was originally sung in honour of Apollo, and seems to be as old as the worship of this deity. The etymology of the word is doubtful. Some suppose that it obtained its name from Paeon, the god of healing ; but in the Homeric poems Paeon is always spoken of as a separate divinity, distinct from Apollo. Other writers, with still less probability, connect it with παίω, to strike.

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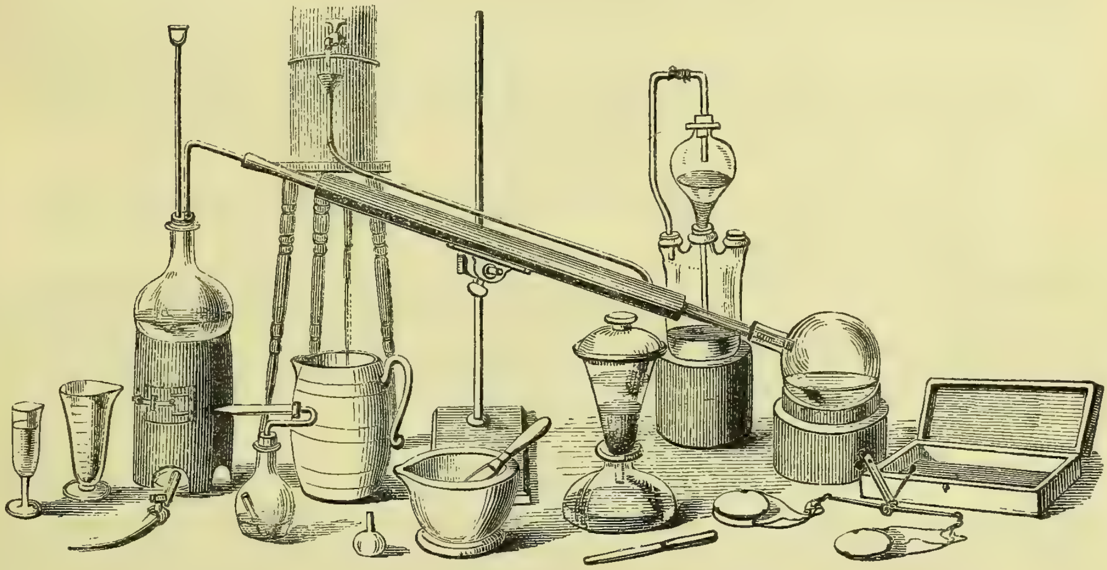

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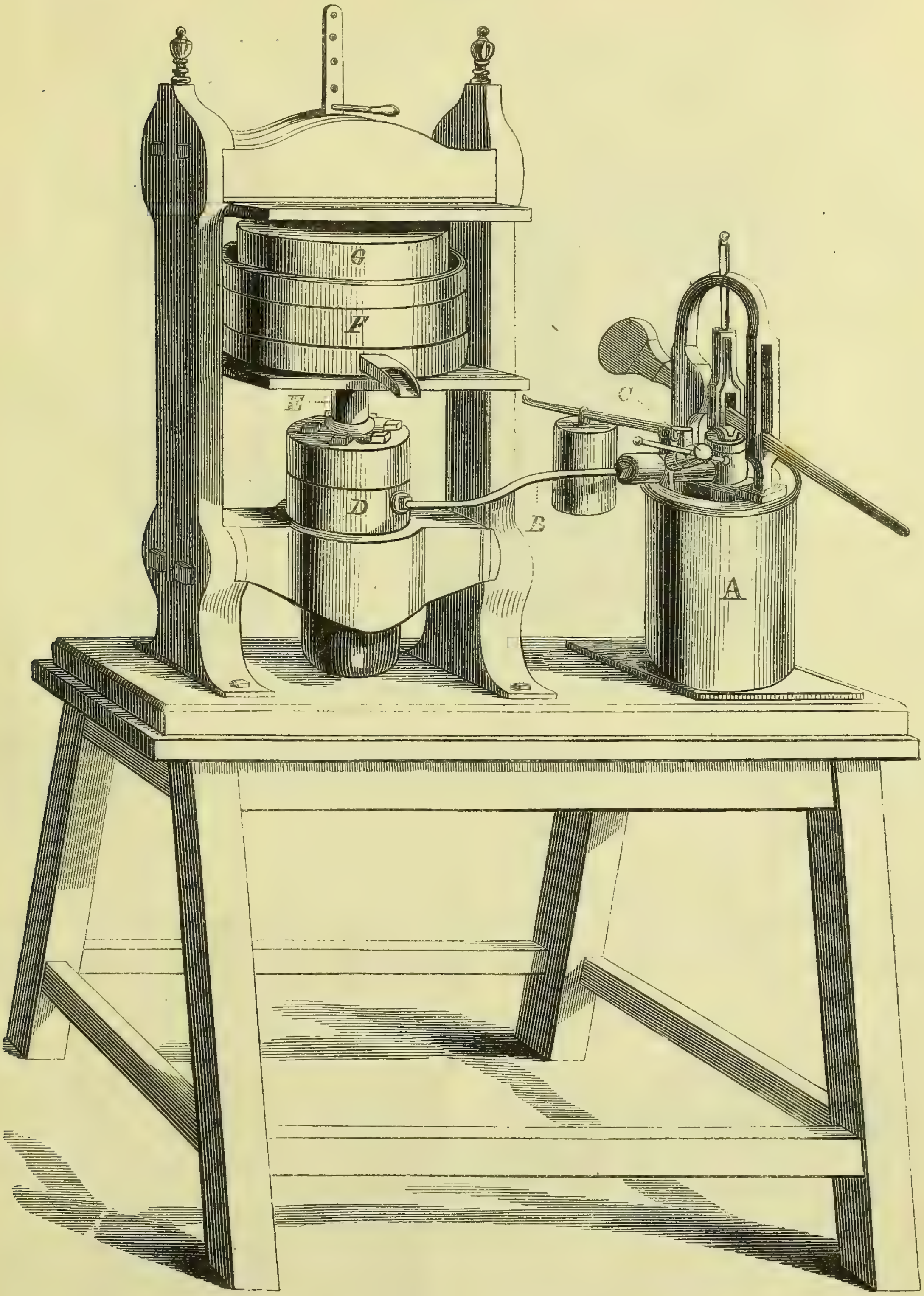
[Specimen of Mohr and Redwood's Pharmacy.]

See page 9 of the preceding List.

BRAMAH'S HYDRAULIC PRESS.

Fig. 100 represents a small hydraulic press, which I have been accustomed to use for several years. The framework of the press is made of cast-iron, and it rests on a strong wooden stand. A, is a cistern containing water, in which is placed a small forcing-pump worked by a lever-handle, which may be lengthened when more power is required. This pump communicates with the strong cast-iron cylinder (D), by means of the metallic tube (B). * * *

Fig. 100.



Bramah's Hydraulic Press.

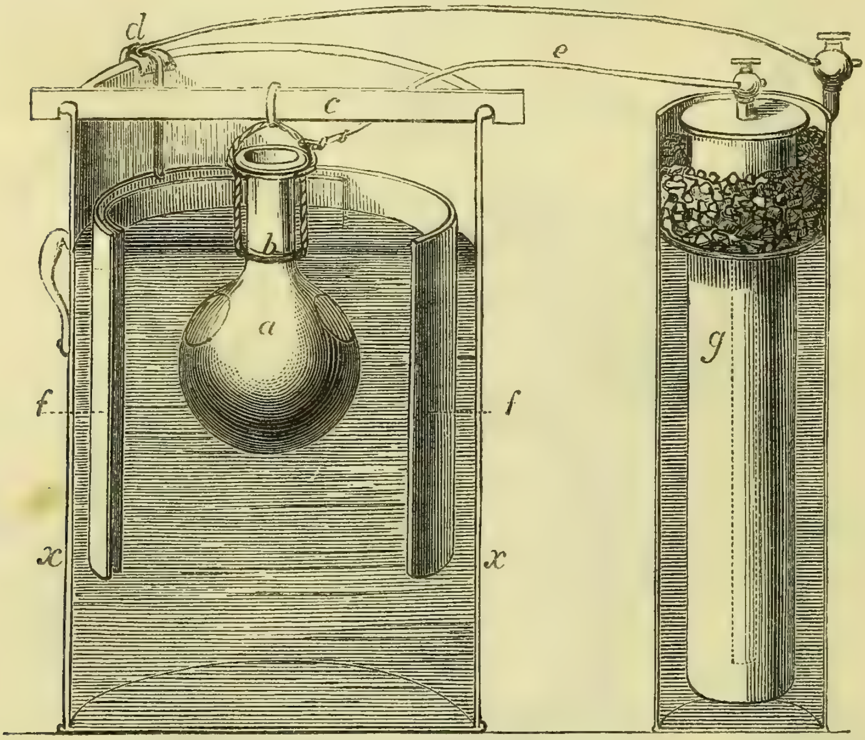
[Specimen of Mohr and Redwood's Pharmacy]

See page 9 *of the preceding List.*

COATING GLASS OR PORCELAIN WITH COPPER.

The arrangement which I have found to answer best is that represented in fig. 371. A thin coating of fat varnish (not spirit-varnish) is, in the first place, applied with a camel's-hair brush, over the part of the vessel on which the metal is intended to be deposited, leaving two or three uncovered circular spaces, as shown on the flask (*a*) in the drawing. * * * *

Fig. 371.



Coating of Vessels with Copper.

PREPARATION OF PILLS.

The covering of pills with gelatine is the most elegant and efficient method of fulfilling the objects contemplated in the processes now under notice. A pill, when thus covered, has a clean, shining, surface, which is dry, hard, and not at all sticky. No powder is, therefore, required in addition to the gelatine. The ingredients of the pill being inclosed in a gelatinous case, are preserved from the action of the air, and, to a certain extent, are prevented from undergoing volatilization; moreover, the pill itself may be swallowed without perceiving taste or smell. * * * *

Fig. 386.

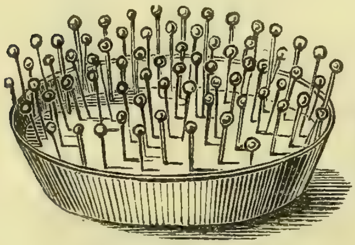
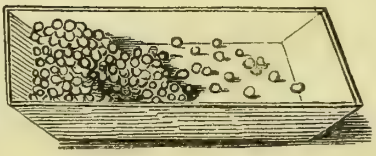


Fig. 387.



Coating Pills with Gelatine.

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